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THE RUSTICA PRESS (PTY.) LTD., WYNBERG, CAPE

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VOLUME 66

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Volume **66** Band
October **1974** Oktober
Part **1** Deel

POPULATION STRUCTURE IN *AGAMA ATRA* AND *CORDYLUS CORDYLUS CORDYLUS* IN THE VICINITY OF DE KELDERS, C.P.

By
BRYAN R. BURRAGE

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

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Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad, 8000

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R4,00

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1974

ISBN 0 949940 54 2

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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By

BRYAN R. BURRAGE

*South African Museum, Cape Town**

(With 5 tables)

[*MS. accepted 1 October 1973*]

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INTRODUCTION

Ecological studies on southern African reptiles have been undertaken since January 1969. This paper describes the spatial and social organization of the *Cordylus cordylus cordylus* and *Agama atra* inhabiting the vicinity of De Kelders, Cape Province.

The ecology of many American reptiles has been investigated to the point where general tenets and recognition of organizational patterns can be made (Carpenter 1967; Rand 1967; Ruibal 1967). The same cannot be said of Old World forms, though North African and Australian studies are filling in the picture. It seems proper to improve our knowledge of southern African forms.

Little has been done on the overall systematics of southern African lizards since FitzSimons's (1943) excellent work. The identity and relationships of some forms are confusing. Before worth-while ecological work can be done, it is important to identify properly just what species are being worked on.

MATERIALS AND METHODS

Populations of *Cordylus cordylus cordylus* and *Agama atra* were studied on 10 hectares of coastal cliffs, 2 hectares of inland rock outcrops, and almost 2 hectares in sandy situations (0,7 ha isolated rocks on sand; 1,188 ha isolated

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Ann. S. Afr. Mus. **66** (1), 1974: 1–23, 5 tables.

koppies amongst sand dunes). Lizards were captured by 'chase and grab', can-trapping, or stunning by being shot with a rubber band cut from an inner tube. These animals were then marked (see Table 1) by toe-clipping and branding with an identification number. Animals were observed from vantage points by means of binoculars. Points visited by a lizard were marked at the site with a rock on which the lizard's number, sex, and observation data were printed in waterproof ink. The points were simultaneously plotted on a scaled map on graph paper of each study area. The denser the dots, the greater the activity of the lizard within a given part of its occupied area, and the peripheral dots on the map and site markers gave the exact area. Peripheral markers were small tripod rock cairns upon which a rock (with identity markings) pointed to the centre of a given occupied area. Connecting the outlying dots gave the periphery of the occupied area, the extent of which was then computed with a planimeter from the graph paper. Social interactions were marked on the site where they occurred and on the graph paper to determine usage of a given occupied area and what part(s) were most vigorously defended. Territories and home ranges were computed only on the basis of ten or more captures per lizard.

Table 1

Cordylus cordylus cordylus and *Agama atra* marked by toe-clipping at various study stations March 1971 to September 1972.

Study station	*Juveniles*	*Adults* ♂♂	♀♀	*Total*
Coastal cliffs				
Agama atra	620	78	77	775
Cordylus cordylus	406	82	83	571
Inland rock outcrops				
Agama atra	204	25	26	255
Cordylus cordylus	312	52	52	416
Rocks among dunes				
Cordylus cordylus	248	113	111	472

DESCRIPTION OF TERRAIN

The Walker Bay coast from the rocky cliffs at De Kelders, north into the dunes is the study area. The rocky cliffs are mostly of the Table Mountain Series, composed of sandstone, quartzite, conglomerate, and shale. To the north are cliffs and outcrops of calcareous dune sand of the Bredasdorp Beds. While there are some sheer cliff faces to seawards, cliffs of the Table Mountain Series often present a sequence of step-like ledges. Cliffs of the calcareous dune sand present somewhat the same aspect, but with greater overhanging ledges. The old dune bedding planes are quite clear. Immediately landwards of the cliff edges are small outcrops which appear as step-like tables.

The shifting dunes are composed of white sand and are arranged in roughly north–south longitudinal series. Among the dunes immediately on the maximum high tide line are some rock outcrops. Further inland among the dunes are scattered rock koppies of varied size, but of essentially similar configuration. There are small koppies (Table 2: koppies 'A' & 'B') not exceeding 2 m in height, which may be one unit, as are the larger koppies, or discontinuous with intervening sand. The larger koppies present an appearance of jumbled terraces (the 'Tiers' of koppie 'C' in Table 2) at different heights from ground level to less than 5 m high. Also, amongst the dunes are scattered large flat rocks, none of which is more than 1 m high. At the eastern edge of the dune area, and in some places extending into the dune area in finger-like projections, are sandy, brush-covered hummocks, some having a rock outcrop core.

This area lies in the winter-rainfall area of the coastal western Cape. The vegetation is Coastal Macchia (Acocks 1953), consisting of shrubs, grasses and other annuals. On the sandy beaches are a variety of succulents. The dunes are devoid of vegetation, except at their bases, but this may be vegetation which they are burying. Some koppies appear to have been exhumed as the dunes move on and these are devoid of woody vegetation, having only a few succulents and grasses. Other koppies seem not to have been recently buried and these have woody vegetation.

The Forestry Department is presently engaged in reclaiming these dunes, destroying this habitat in its current appearance.

OBSERVATIONS AND DISCUSSIONS

THE POPULATION AND HABITS OF THE LIZARDS

Agama atra is commonest (155 adults per hectare) on the bare rock surface of the coastal cliffs, and occurs sparsely (51 adults per hectare) on isolated bare, flat rock outcrops surrounded by open shrub. It is absent on rocky outcrops surrounded by dense scrub or large expanses of sand, and on the koppies and rocks amongst the dunes. Juveniles of varied age groups are up to four times as dense as the adults.

Cordylus cordylus cordylus occurs in all of the above habitats, as long as there are some rocks, which are the focal point of its activity and in which the lizards have their retreats. Those inhabiting the coastal cliffs are predominantly of a yellowish-phase, but only brownish-gray ones inhabit suitable habitats among the dunes. On the terraces of large rock koppies the population density of adult cordylids is as high as 288 per hectare, and as low as 4,2 per hectare in the area of isolated rocks on sand. Juveniles of varied age groups are two to three times as dense as the adults. The adult population density of both species in the various habitats is given in Table 2.

While the spatial organization of *Agama* appears unvarying, that of *Cordylus* differs according to the habitat. *Agama* and *Cordylus* co-inhabit the coastal cliffs, but competition is lessened by the different thermal requisites of each and, hence, different activity patterns. *Cordylus* is abroad in the early morning and late afternoon on sunny days, and abroad throughout the day under overcast conditions. However, *Agama* prefers higher temperatures and is most active when *Cordylus* has sought the cool of its shelters.

THE TERRITORIES AND HOME RANGES

Agama atra adults of both sexes are typically territorial (Table 2). Despotism occurs among the more crowded populations along the immediate shore. Despotic individuals are males, almost invariably those with the largest territories in this situation. Territorial borders are usually delimited by ledge edges, fissures, and the like. The highest part of all territories is the focal point, allowing the occupier a vantage site for surveying its domain. The vertical area is greater

Table 2

Particulars of the spatial organization of *Agama atra* (Aa) and *Cordylus cordylus cordylus* (Cc) in the vicinity of De Kelders, Cape. All areas shown are in square metres. 'T' denotes territory and 'HR' denotes home range in the table. Only the N of Territory and/or home range holding adults with a minimum of 10 recaptures is shown (compare with Table 1).

Species	♂♂	♀♀			*Adults per hectare*	*Koppie*	*Type of social organization*
	Coastal cliffs						
Aa. . .	N=67 78,0–188,5 (92,5)	N=68 22,5–91,5 (56,0)			125,0	—	T
Cc. . .	N=75 65,6–124,5 (90,0)	N=76 33,2–100,0 (80,0)			165,0	—	T
	Inland rock outcrops						
Aa. . .	N=20 98,8–250,0 (120,0)	N=20 32,5–105,0 (77,0)			51,0	—	T
Cc. . .	N=46 70,0–130,0 (110,0)	N=45 60,7–100,1 (82,6)			104,0	—	T
	Koppies situated in dunes. Adult ♂♂ and ♀♀ share a territory and/or home range with their juveniles.						
Cc (only)	♂♂	♀♀					
	N=6	6	4,0–20,5 6,0–16,0	(14,1) (10,7)	74,4	A	T HR
	8	8	4,0–22,0 4,0–20,0	(13,7) (11,4)	230,4	B	T HR
	26	22	4,0–16,0 4,0–20,0	(8,5) (9,6)	110,4	C Tier I	T HR
	10	12	4,0–16,0	(8,9)	244,2	C Tier II	HR
	24	24	4,0–10,0	(7,0)	288,0	C Tier III	HR
	20	18	4,0–12,0	(7,1)	285,0	C Tier IV	HR
	4	6	4,0–12,0	(7,6)	260,0	C Tier V	HR
	Isolated rocks situated in sandy areas. Adult ♂♂ and ♀♀ share a territory with their juveniles.						
Cc (only)	♂♂	♀♀					
	N=7	7	84,0–180,0*	(108,9)	4,2		T

* Does not reflect a litigated area of 18,0 m^2 between two *Cordylus* groups, nor changes in territory sizes after the removal of Group 1 (see Table 3).

than the horizontal, allowing more effective surveillance of a larger territorial area than could be realized if the territories were arranged along a contour. While such an arrangement is favoured by the topography, it allows more agamids to maintain effectively larger territories than could be realized on flat areas. Unfortunately, maps drawn in plan view do not accurately reflect those areas in steep slope.

Territories extend seawards almost to the water's edge, the *Agama* including various intertidal arthropods in its diet. All male territories are larger than those of the females, and each male has a group of two or three females. The smaller territories of the females are wholly or mostly within that of the male. Members of each group have their preferred resting-spots. Females within the territories of despotic males seem to be more aggressive in defending their respective territories from other females of their male's territorial group, but markedly so against females of another male (see also 'Social Interactions') especially those of the non-despot males. The development of despotism in such areas may indicate that the population pressure is reaching the limits for a territorial organization. If the population pressure increases, so much time may be spent in territorial defence as to be detrimental to the well-being of the species. Creation of a hierarchical structure or despotism would reduce or eliminate antagonistic behaviour. With greater population pressure, a social organization of 'free-run' could be expected. Another alternative would be the reduction of territories to a certain size and the stabilization of population size.

Territories of *A. atra* are largest in areas with lower population densities. The nature of the topography seems to allow the coastal agamids to establish and maintain larger territories than the high population density would allow on areas of a flatter or more uniform topography.

A study of an intertidal population of *Agama atra*, *Mabuia capensis* and *M. homalocephala* inhabiting scattered rock along the Rooi Els River mouth and beach showed that agamids are limited to such rocks as occur, and many occupy larger territories than is reported here. This is especially true of those occupying scattered rocks right at the water's edge and isolated from other suitable habitat by sand or dense brush. In this situation there is no despotism.

Cordylus cordylus has a higher population density on coastal cliffs and territories of both sexes are smaller than those on inland rock outcrops. In all situations female territories are smaller but rarely overlap those of more than one male (see also 'Social Interactions'). The sexes do not form groups in the manner of *A. atra*. *C. cordylus* digs a burrow, usually located in a redoubt, as in the soil deep in a rocky crevice. In their burrows they are virtually secure from any danger, since they inflate the body, grasp the sides of the burrow with their clawed feet, and present the spiny tail to the intruder. The delimitation of *C. cordylus* territories closely follows that described above for *A. atra* in these situations.

In dune and sandy areas *C. cordylus* occurs in isolated population subunits, closely connected to koppies or areas of scattered rock. The social organization here is quite complex and obviously closely regulated to the rocky habitat they prefer. Each territory or home range is occupied by an adult male and female along with their juveniles of varied age groups. In the territories the adults of both sexes fiercely defend their area against intrusion by any lizard of any age group. In the presence of adults, the juveniles sometimes assist in the defence of the area. In the home ranges, each group has its own foraging area but transients are tolerated. Burrows of each group are always defended. In home ranges and territories the retreats are located in rocky crevices or burrows and are occupied by the entire group. Such burrows have a narrow entry way and very large, often branching terminal enlargements. Thus, the *C. cordylus* 'family group', where it occurs, is a tighter organization than that of *A. atra*.

On small koppies ('A' and 'B' in Table 2, and see also pp. 16–17) *C. cordylus* has a territory and home range with the territory on the periphery. The territory includes some of the rocky area, but mostly it is a skirt of sand of varying width around the koppie. The lizards' burrows are located in the rocky area. One group in koppie 'B' had only a territory. Two groups in koppie 'C' and one group in koppie 'B' had only home ranges. Those maintaining only home ranges were located more or less in the centre of the koppies, being completely surrounded by other cordylids. The borders in koppie 'C' closely follow the demarcation by large blocks of rock, but in the more scattered koppie 'B' the borders are more arbitrary.

The spatial organization of *C. cordylus* on koppie 'C' closely follows the step-like arrangement of koppie 'C'. Thus, they can be arranged in tiers from the periphery (Tier.I) of the koppie, to each successively higher terrace, inwards to the centre (Tiers II–V). On this koppie only the 24 groups of Tier I maintain a territory and home range, being territorial on the periphery, with the home range on the rocky area. The territories consist only of a sandy area of varying width, mostly narrow and especially so on the western edge of the koppie where a large dune closely abuts. The population density increases inwards and the size of the home ranges diminishes. Slight deviations from this trend are due to larger rock blocks at the centre, possibly influencing border demarcation and the density of lizards to occupy such home ranges. Borders of home ranges closely follow that of the jumbled large rocks. That is, a home range is limited to one large rock or associated rocks on each tier.

Population density varies inversely with territory size. Such territories occur on sandy areas with scattered large rocks, and on sandy hummocks with rocky core and brush cover. Generally speaking, those territories on sandy areas with scattered large rocks were larger than those situated on the hummocks. These cordylids maintain only rigidly defended territories. The centre of activity is on the scattered rocks, especially those in which their burrows are located. They do forage over the sand between the rocks within their territory. Five of the seven such *C. cordylus* groups had borders abutting on others. The two *C. cordylus* groups with the largest territories (Group 1: 180,0 m^2, and Group 2: 116,0 m^2, respectively) often disputed a litigated border area of 18,0 m^2 along a dry wash on their borders. The reason for the dispute is not clear, since the dry wash is mostly hard sand, having no rocks of any size to battle over. Since its ownership alternately shifted and its integrity apart was sometimes mutually observed, I consider it a 'buffer zone'. *C. cordylus* Group 3 occupied a 100 m^2 territory situated in a sandy area with rocks but had no common border with any other *C. cordylus* group. Situated on the hummocks were Group 4 with 104 m^2 (partly bordering on Groups 1 and 5), Group 5 with 94 m^2 (bordering on the territories of 1 and 4), Groups 6 and 7 with 84 m^2 each, of which only Group 6 bordered partly on Group 5.

The removal of both adult cordylids, plus some juveniles of Group 1, resulted in an interesting adjustment for the surviving juveniles and reapportioning of this territory amongst the surrounding groups. This reapportioning can be divided into three stages over 120 days, details of which are given in Table 3. In the first stage Group 2 took over the litigated area and 72 m^2 of the territory of Group 1, including most of Group 1's retreat rock, its 1 m high pinnacle and another rock. Group 4 took over 16 m^2 of the territory of Group 1, and while mostly borderland it included a part of Group 1's retreat rock, but not the burrow or pinnacle. Group 5 took over 56 m^2 of the territory of Group 1, consisting mostly of sand and one rock, quite isolated from its original holdings. This arrangement lasted for about a month, and over the subsequent three weeks further adjustments occurred, largely in the favour of Group 2.

It is somewhat interesting that Group 2 maintained the integrity of its

Table 3

Territorial changes of *Cordylus cordylus cordylus* groups (Nos 1–7) inhabiting isolated rocks in sandy areas. Each group composed of one adult male and one adult female and a number of juveniles (see Table 1). After the removal of the adults of Group 1, the acquisition is shown of Group 1 territory by the other groups, with their new total territories in parentheses. All areas shown are in square metres.

	November		*30 days later*	*March* *120 days later*
Groups	Initial	Stage 1	Stage 2[c]	Stage 3[d]
1	180[a]	some removed	—	128
2	116[a]	+90 (106)[b]	+20 (226)[b]	134[b]
3	100	no change	no change	no change
4	104	+16 (120)	+8 (112)	104
5	95	+56 (151)	+44 (139)	95
6	84	no change	no change	no change
7	84	no change	no change	no change

[a] = Does not include litigated area of 18,0 m^2.
[b] = Includes litigated area of 18,0 m^2.
[c] = In stage 2, Group 2 added Group 1 territory taken by Groups 4 and 5, their reduced acquisition of Group 1 territory is shown.
[d] = In stage 3 the surviving Group 1 juveniles had evicted Groups 2, 4 and 5 from the former territory of their adults.

swollen territory, even though it seemed difficult to defend. That is, its original central rock with the retreat burrow was located more in the western extreme of its territory; quite far removed from the eastern limits of its annexations of Group 1 land, located closer to the territories of Groups 4 and 5. Also, the territory of Group 2 bordered on two territorial groups in Tier I of koppie 'C', neither of which was observed to intrude into Group 2 territory.

More interesting was the surviving Group 1 juveniles, who in the absence of their parents and some of their peers, did not make any obvious attempts to maintain any territorial integrity of the whole or part of the Group 1 territory. It could be assumed that they could not defend it in the manner or to the extent that the adults did, but their defending the central rock (about 16 m^2) and retreat burrow would seem barely plausible. Group 1 juveniles were apparently taken over, integrated with, or just ignored by the successors to their parents' territory. During and after the stabilization of the situation, Group 1 juveniles continued to occupy the area, though they seemed limited to an area of about 20 m^2, mostly concentrated to the central rock. They were not challenged, but seemed submissive in the presence of *C. cordylus* from the other groups which had annexed parts of Group 1 territory. They did continue to utilize their own retreat, which, on occasion was also occupied by *C. cordylus* of Group 2. The latter, however, did not occupy the Group 1 retreat on a permanent basis and maintained their own retreat. It hardly seemed conducive to lizard occupancy to disturb the retreats too often.

In March 1972 the area was reinvestigated, with the interesting discovery that the newly mature older Group 1 juveniles had acquired territorial desires and had reclaimed and were successively defending most of their old Group 1 territory (128 m^2), except an area of mostly sand with two small outlying rocks, which was little used even when their parents were present. Groups 2, 4 and 5 individuals had been totally evicted from Group 1 territory, but Group 2 integrated the former litigated area into their territory. Group 2 territory was not what it was when first studied.

Examination of *C. cordylus* territorial organization in other koppies, hummocks and sandy areas with scattered rocks follow the same pattern described above for that investigated in detail in the particular study site. While no detailed investigation was undertaken of *C. cordylus* territories in the rocky, sandy beach areas in the supratidal area, it appears to follow that of the dune sandy areas with scattered rocks.

Juvenile cordylids on coastal cliffs and inland rock outcrops have 'free run' of adult territories, but gradually disperse as they mature and take up territories where they can defend an area. In both *Agama atra* and *C. cordylus* there appears to be a 'phantom population', mostly of recently matured adults, that does not defend a territory, possibly because it cannot find a place to defend due to those already ensconced. In rocky situations the 'phantom population' has a reasonable chance of surviving until vacancies occur. On isolated rocks in sandy areas juvenile cordylids disperse as they mature and try to set up a territory of their own, which seems to be a difficult task as almost all available sites are occupied. Since maturing juvenile males are evicted if they show interest in the female (their mother) of the adult male (their father), they are forced into a hostile environment (sand) to disperse to any area that can afford them shelter to survive. Many succumb to predators. In this habitat the 'phantom population' is almost theoretical. Maturing males of these isolated rocks are virtually dependent on the death of their adults (particularly their father) if they are to survive and establish their own territory. The pressure on maturing juvenile females is less, but the adult female (their mother) will evict them if they show interest in their father. For those on the large koppies this pressure on newly matured cordylids is less intense.

The spatial relationships of American iguanids have been studied most, and good reviews are those of Carpenter (1967), Rand (1967), Ruibal (1967) and Mayhew (1968). Most lizards have a 50:50 sex ratio.

Of Old World lizards Harris (1964) reports a density of *Agama agama* 36 per acre (90,0 per hectare). Burrage (1973) found the population density of the mesic *Chamaeleo pumilus* to vary from 12 adults per hectare in brushy areas to 75–200 adults per hectare on reeds surrounding still bodies of water, with males averaging 43% of the population. However, population density in arboreal forms (e.g. *Anolis* and *Chamaeleo pumilus*) is three-dimensional, not in plan as with ground-dwelling species. The ubiquitous, ground-dwelling, deserticulous *C. namaquensis* is most numerous in topographically varied areas, with a mean annual density of 51,8 adults per hectare, with a sex ratio slightly favouring females.

Of New World lizards, population density in some, e.g. *Uta stansburiana* and related insular forms of *Uta* (Soulè 1964); *U. s. hesperis*, *stejnegeri* and *elegans* (Burrage 1966); *U. s. stansburiana* and *stejnegeri* (Tinkle 1961, 1967; Tinkle, McGregor & Dana 1962; Tinkle & Woodard 1967), varies from an average inland density of approximately 25,5 territory-holding adult utas per acre (approximately 63,8 per hectare) to littoral and insular populations two to three times as dense. In some unusual conditions some mainland *Uta stansburiana* populations may be as much as 700 per acre (1 750 per hectare) in Utah (Knowlton, Fronk, & Maddock 1942); in California and Mexico (Burrage 1966); in Colorado (Ferguson, pers. commun.)). Burrage (1966) found that the population density of *U. s. hesperis* varies according to the topography and to a lesser degree the plant density of the particular locales studied. *U. s. hesperis* population densities vary from 20,0 to 750,0 ($\bar{x} = 179{,}5$) adults per hectare in areas altered (e.g. steeply graded, or terraced, a greatly reduced plant density of usually uniform type, chiefly weeds in the early stages of plant succsssion) by human activity. On the undisturbed backshore of topographically rugged or varied beaches with a low plant density there are 55,0 to 62,5 ($\bar{x} = 59{,}0$) adult utas per hectare, 37,5 adult utas per hectare in beach canyons, and 30,0 to 47,5 ($\bar{x} = 32{,}5$) adult uta per hectare in inland areas. Beach areas are topographically varied and intricately eroded, allowing a higher population density than can be realized on flat terrain. Disturbed areas and beaches have scattered plants in which are abundant prey concentrations. Tinkle (1967) found that *U. s. stejnegeri* in Texas concentrates its activity around *Neotoma* (wood rat) nests—a rich source of arthropod prey—which are sited in *Prosopis* (Mesquite) clumps. Jorgensen & Tanner's (1963) Nevada data suggest that the prey of the *Uta s. stansburiana* is more dispersed, and/or the topography more uniform, the plants more dispersed, and so are the lizards.

Very few tropical lizards have been studied, but Heatwole (1967) mentions *Anolis limifrons* having a population density of 400 per acre (approximately 1 000 per hectare) and refers to Turner & Guest finding densities of >600 per acre (approximately >1 500 per hectare) for *Anolis gunlachi*, a medium-sized anole of Puerto Rican montane rain forests. Cagle (1946) reports a density of 500 adult *Hemidactylus* (Gekkonidae) in a 2 400 ft^2 (approximately 223,2 m^2) area on Tinian, so assuming an even distribution this gives 10 000 per acre (25 000 per hectare). Hirth (1963) studied the ecology of a teiid (*Ameiva quadrilineata*) and an iguanid *Basiliscus vittatus* on a Costa Rican beach. He found the density of juveniles of the former species varies from 12,6 to 24,2 per hectare, and the adults from 17,1 to 39,1 per hectare, the combined numbers suggesting a teiid population of 29,7 to 63,9 per hectare. Juveniles of *B. vittatus* vary from 13,8 to 27,9 per hectare. The adults of this species are only 5,2 to 10,9 per hectare, owing to the fact that they did not especially frequent the study area and do not compete with their juveniles. Actually, adult *B. vittatus* density would be at least double. For *B. basiliscus* in the Panama Canal Zone, Barden (1943) estimates a population density of one lizard per 15,2 m of shoreline.

Regarding spatial organization of lizards, some authors confuse the issue by using 'defended home range' instead of 'territory', justifying such disconcerting usage because the home range of a particular species is also its territory. While a 'defended home range' is synonymous with 'territory', the same authors omit the word 'defended' in their discussion, when it should be included. Since in some parts of their distribution the same species can also possess a territory (defended) and a home range (undefended), it is too cumbersome to speak both of a 'defended home range' and a 'home range'. Needless confusion results from those who use only home range when obviously territory is the correct term. Thus, I feel use of 'defended home range' should be dropped in favour of 'territory', and in no case should 'home range' be used for any area defended by any species. Table 4 gives the mean territory and/or home range sizes of some of the lizards reported in the literature.

Discussions of spatial occupancy in lizards are disconcerting, because of varied techniques employed, consideration of widely separate populations in different habitats, physical factors (varied geologic substrates, local topography), and biotic factors (e.g. population density of the studied species, competition, plant density). Few attempts have been made to study adjacent populations of the same species in the same general area under slightly different conditions of local topography (e.g. relief, slope angle), types of geologic substrates, plant

Table 4

Review of mean territory and home range sizes of some of the lizards reported in the literature.

			Area occupied			
Species	*Sex*	*Age*	*Acres*	*Metres^2*	*Remarks*	*Source*
Amblyrhynchus cristatus	♂♂	adult	—	1,0	Only in breeding season	Carpenter (1967)
	♀♀	adult	—	—	Only displays	Carpenter (1967)
Ameiva quadrilineata	♂♂	juvenile	—	16,4		Hirth (1963)
	♀♀	juvenile	—	15,1		Hirth (1963)
	♂♂	adult	—	21,1		Hirth (1963)
	♀♀	adult	—	13,7		Hirth (1963)
Anolis sagrei	♂♂	adult	—	36,0		Evans (1938)
Basiliscus vittatus	♂♂	juvenile	—	14,9		Hirth (1963)
	♀♀	juvenile	—	12,4		Hirth (1963)
	♂♂	adult	—	12,0		Hirth (1963)
	♀♀	adult	—	12,2		Hirth (1963)
Chamaeleo namaquensis	♂♂+♀♀	juvenile	—	27,5		Burrage (1973)
	♂♂	adult	—	1 717,5	Coastal	Burrage (1973)
	♂♂	adult	—	1 250,2	Inland	Burrage (1973)
	♀♀	adult	—	382,0	Coastal	Burrage (1973)
	♀♀	adult	—	867,9	Inland	Burrage (1973)
Chamaeleo pardalis	♂♂+♀♀	adult	Several	10 m^2		Bourgat (1968)
Chamaeleo pumilus	♂♂+♀♀	adult	—	600,0		Burrage (1973)
Cnemidophorus hyperythrus	♂♂	adult	0,07	283,3		Bostic (1964)
	♀♀	adult	0,10	404,7		Bostic (1964)
Cnemidophorus tigris	♂♂+♀♀	juvenile	0,09	364,2		Jorgensen & Tanner (1963)
	♂♂	adult	0,50	2 023,5		Jorgensen & Tanner (1963)
	♀♀	adult	0,24	971,3		Jorgensen & Tanner (1963)
Ctenosaura pectinata	♂♂+♀♀	adult	—	2,1		Evans (1951)
Sceloporus olivaceus	♂♂	juvenile	0,027	109,3		Blair (1960)
	♀♀	juvenile	0,017	68,8		Blair (1960)
	♂♂	adult	0,17	687,9		Blair (1960)
	♀♀	adult	0,07	283,3		Blair (1960)
Uta stansburiana hesperis	♂♂	juvenile	0,005	20,2	California	Burrage (1966)
	♀♀	juvenile	0,004	16,2	California	Burrage (1966)
	♂♂	adult	0,05	202,4	Calif. coastal	Burrage (1966)
	♀♀	adult	0,034	137,6	Calif. coastal	Burrage (1966)
Uta stansburiana hesperis	♂♂	adult	0,075	303,4	Calif. inland	Burrage (1966)
	♀♀	adult	0,056	226,6	Calif. inland	Burrage (1966)
	♂♂	adult	0,021	85,0	Intertidal home range of stranddwellers	Burrage (1966)
	♀♀	adult	0,016	64,8		Burrage (1966)
Uta stansburiana stansburiana	♂♂+♀♀	juvenile	0,04	161,9	Nevada	Jorgensen & Tanner (1963)
	♂♂	adult	0,10	404,7	Nevada	Jorgensen & Tanner (1963)
	♀♀	adult	0,03	121,4	Nevada	Jorgensen & Tanner (1963)
Uta stansburiana stejnegeri	♂♂	adult	0,11	444,2	Texas	Tinkle (1967)
	♀♀	adult	0,03	121,4	Texas	Tinkle (1967)

density, and lizard population density. Burrage (1966) conducted a five-year investigation of spatial occupancy in *Uta stansburiana hesperis* populations in southern California at selected, proximal study stations of varied location and topography (e.g. coastal bluffs, sandy and rocky beaches, coastal and inland canyons, rugged and flat topography), geologic substrates, plant density and populaton density. He found widely different territory sizes and social organizations obtaining at each study station to a degree reported as 'standard' for this species by Jorgensen & Tanner (1963) at one site in Nevada, and Tinkle, McGregor & Dana (1962) in an area of Texas. Thus, environmental factors in widely separate areas could account for an actual difference in territory size (see Table 4) rather than computation error (Jorgensen & Tanner used density probability function, obtaining larger territory sizes than Tinkle *et al.* using the minimum polygon method). Furthermore in Texas, utas concentrate their activity around *Neotoma* nests in *Prosopis* clumps and, thus, have less need to wander for food than the utas in Nevada, probably resulting in smaller Texas *Uta* territories than those in Nevada.

Furthermore, as Tinkle (1967) observes, there are few studies based on large numbers of captures. Also, despite the studies demonstrating territorial behaviour in lizards (mostly temperate iguanids), there has been little speculation as to its adaptive significance in reptiles, as has been done by Nice (1941), Hinde (1956) and Carpenter (1958) for other animals, mostly birds. Rand (1967) has made a step in this direction, based largely on his observations of the iguanid *Anolis lineatopus* on Jamaica. Hypothetical values of territory can be: (1) securing a requisite share of environmental resources, and/or (2) mating, and/or (3) survival of offspring. Rand reports that the critical environmental resources for *A. lineatopus* need be defended intra- and interspecifically. Food is the limiting resource for other lizards, such as *Sceloporus merriami* (Milstead 1961) and in such cases both sexes defend.

Defence only of the resting site is noted (Knowlton *et al.* 1942; Burrage 1966) in *Uta stansburiana* populations too large to permit or necessitate territorial establishment; as areas with abundant and/or concentrated prey. *U. s. hesperis* maintains territories in the backshore areas of beaches, but has only home ranges intertidally, where the variety and numbers of food are greater.

There are paltry data on spatial organizations of Old World lizards. Harris (1964) gives territory sizes of 600–900 ft^2 (58,8–84,6 m^2) for male *Agama agama* in population densities of 36 adults per acre (90 per ha). Harris noted that dominant females never leave dominant males. Several adult females occurred with each dominant male, one female being dominant and 'true' to the male. Subdominant females will desert. All juvenile males leave the area they occupy as hatchlings, but young females may remain.

Bourgat (1968) gives an area of 'several 10 m^2' for the home range of *Chamaeleo pardalis* on Reunion. Burrage (1973) found that *C. pumilus* has a home range of 10 m^2 in plan, but since the space is three-dimensional, the actual area covered is closer to 600 m^2. *C. pumilus* only defends its night-time resting perch, the security of which is important to this species. This observation is true of other arboreal chamaeleons (Brain 1961; Bustard 1958, 1965, 1966, 1967; Von Frisch 1962; Spence 1966).

In the ground-dwelling, deserticulous *C. namaquensis*, most territories embracing different habitats are larger than those limited to one. The largest male territory was 8 000 m^2; the largest female territory was 1 632 m^2. Territory size in this species varies according to reproductive demands, with male territories increasing in area during courting and those of females during egg-laying. Male territories, however, are always larger than those of females and were surrounded by more smaller female territories than they bordered on those of other males. As with other chamaeleons, *C. namaquensis* has a more or less centrally located resting-area, usually in a redoubt. Unlike most lizards, *C. namaquensis* territories do not have areas of greater or lesser usage. On waking in the morning *C. namaquensis* patrols to the border limits and encompasses its entire domain. With the passage of time, *C. namaquensis* patrols its territories in decreasing circuits inwards to the rest area. The border configuration of *C. namaquensis* territories is especially interesting, for finger-like projections of the territory of one chamaeleon intrude into that of another. In areas of micro-relief, as hummocks, such projections closely followed the high ground, but this curious system prevailed even on monotonously flat areas, and especially on dunes, where one would suspect territories to be circular or squarish, since there was no micro-relief or landmarks to regulate border configuration. Maintenance of territories in *C. namaquensis* assured that any one male could meet several females during the normal diel patrol of both sexes. Also, vigorous territorial defence by the female *C. namaquensis* would prevent exhumation of the defending chamaeleon's buried eggs by other females seeking to build a nest. Each female *C. namaquensis* constructs its nest only within the borders of its territory.

In the case of *Agama atra* and *Cordylus cordylus* on coastal and inland rocky outcrops, territorial establishment is best interpreted as enforcing a spacing of the population for the most efficient use of available resources. Closer to the sea, there is a reduction of available area, but an increase in the numbers and variety of prey favours a trend to despotism in the slightly larger local population of *Agama*.

Cordylus cordylus in the inner tiers of the rock koppies has populations too large to establish or maintain territories successfully and shelter is not at a premium and possibly also food. This is not so for those living on isolated rocks in sandy areas. Here, suitable habitat and retreats, and possibly food, are at a premium, and each family group vigorously defends its territory from intrusion by others. This, however, should not obscure the possibility that the cordylids are limited only to the rocky situations because suitable or sufficient supplies of their food are.

I have fully discussed the relationship of juvenile cordylids to their adults. Freshly-hatched agamids of both sexes initially site within the territories of their parents. A few weeks after hatching, juvenile males occupy a shifting home range, gradually dispersing out and away from their parents. They are not free from challenge by adults whose territories they transgress, but are neither evicted. Juvenile females are not free from challenge from the adults, but it seems more recognitory and they are not evicted. Harris (1964) made similar observations for juvenile agamids.

Burrage (1973) reports that the juveniles of the ground-dwelling *Chamaeleo namaquensis* occupy shifting home ranges (10–53 m^2; $\bar{x} = 27{,}5$) occurring wholly or partly within the strongly defended territories of the adults (initially, that of their parents), from whom they are free of challenge. As the juveniles of *C. namaquensis* matured, they began defending their area as they stabilized its location. By shifting an undefended space when juvenile and free of challenges, they might find an unoccupied area they can defend in adulthood. Juveniles always slept on a raised object, such as a twig, and not necessarily the same object each night, and companionably together. Juveniles of *C. pumilus* have no regular sleeping area in the prolonged temporal sense and a continuously shifting home range. Resting *C. pumilus* juveniles are well spaced on twigs or grasses and are hostile to any other chamaeleon being near them. Even new-born young execute vigorous displays. Only captive *C. namaquensis* juveniles displayed and evinced ownership in the presence of food. A sort of 'dog-in-the-manger' affair, where one would be eating in the food dish and vigorously prevent any other chamaeleon(s) from sharing the meal.

In most cases juvenile lizards have smaller territories or home ranges than adults. The exceptions, as Hirth (1963) reports for *Ameiva* and *Basiliscus*, are in Tinkle's (1967) view due to calling a home range a composite of areas occupied by a young animal as it disperses, and it is not the same as a stabilized home range of an adult. This may be so, as if, for example, I had called as stable home ranges the total area occupied by the shifting home ranges of *C. namaquensis* juveniles as they dispersed, the area would surpass the territories of the adults. That a juvenile could or would maintain a larger area than an adult seems quite unlikely. However, I found that the Californian anguids *Gerrhonotus multicarinatus webbi* and *G. multicarinatus nanus* occupy a shifting home range as juveniles and adults. Obviously, this problem needs more thorough investigation. Usually, the role of territories and home ranges in juveniles of a species is overlooked, which is a pity, because understanding spatial relationships at all ages in a given species population gives a far better understanding of the nature of such arrangements to any species.

It is perhaps a mistake to say juveniles are non-territorial, and it would be well to study when juveniles set up territories (see also Blair 1960) with increasing maturity. Burrage (1966) found that juvenile *Uta stansburiana hesperis* had free run of adult territories and was not challenged by the adults and did not exhibit any spatial ownership to each other. Most juveniles of *U. s. hesperis* lived on the domains of adults who were usually their parents; this juvenile to adult association appears to be a loose family unit of sorts. This agrees with

Hunsaker's (1962) report that *Sceloporus*, less than 50% of adult size, was free from challenges. In locales with denser populations, as beach stations, juveniles of *U. s. hesperis* were not usually found to occupy discrete territories, except when a vacancy was created by the death of an adult. For example, at Pacific Beach Bluffs (adult population density 130 per hectare), only four juvenile females occupied territories ranging from 4,1 to 12,1 m^2 ($\bar{x} = 8,1$ m^2). At Alvarado Canyon, a less densely populated (adult population density 62,5 per hectare) locale, 17 juvenile male territories (4,2–28,3 m^2; $\bar{x} = 12,1$ m^2) and 13 juvenile female territories (4,1–16,2 m^2; $\bar{x} = 8,1$ m^2) were present. While a lesser population density favours establishment of juvenile territories in this species, it does not, in itself, guarantee it. Juvenile territories were always located in a redoubt, compact and easy to defend. At Lower Tourmaline Canyon, a beach canyon, with many such redoubts (depression drainage pits associated with the weathering of a particular geological formation), allowed many juveniles to maintain territories, though the adult population density was 75 per hectare. This station had the second greatest number of juvenile territories observed for this species. Seven juvenile male territories ranged from 4,1 to 52,6 m^2 ($\bar{x} = 28,3$ m^2) and five juvenile female territories from 4,1 to 24,3 m^2 ($\bar{x} = 12,1$ m^2).

The territory of any given beach strand-dwelling adult male (N=410) and adult female (N=450) *U. s. hesperis* consists of a small nucleus area (♂♂ $\bar{x} = 20,2$ m^2; ♀♀ $\bar{x} = 12,9$ m^2), where the lizard has its burrow and concentrates its activity; surrounding this nucleus area is a larger defended area (♂♂ $\bar{x} = 178,1$ m^2; ♀♀ $\bar{x} = 105,2$ m^2), with a mean intertidal 'free' zone (home range) of an additional 85,0 m^2 in males; 72,8 m^2 in females. Non-strand utas lacked the home range and are territorial, though it is subdivided as above. By temporally studying establishment of spatial occupancy in this species, the nucleus area of the adult territory is seen to be that area the occupying lizard can initially successfully defend when a maturing, older juvenile. Over this nucleus the maturing juvenile exercises ownership of and is active over an increasingly wider area. It is more selective to success (of territorial establishment) and survival if the lizard initially defends a small, compact area in a redoubt (i.e. stone rubble, thorny xeric plants, or both, etc.) in which it has a retreat, rather than attempts to dominate a larger adult-sized area lacking or devoid of shelter. Juvenile *U. s. hesperis* only begins defending when (1) there is space available, and/or (2) such space is readily defended, as a small compact redoubt, and/or (3) the overall, more importantly, the adult population density is low. As it is more critical for adults in this species to maintain territories, the establishment of territories in this species is a virtual 'right' of adulthood. This is indicated by the dearth of juvenile *U. s. hesperis* territories, and the limited conditions in which they occur. The fact that *U. s. hesperis* juveniles are free of challenge tends to select against the establishment of juvenile territories. In *U. s. hesperis* there is also a 'phantom population' as I have described for *Agama atra* and *Cordylus cordylus*.

While territorial formation is common in iguanids and some agamids (Carpenter 1967), it does not occur in some, as the iguanid *Phrynosoma* (Lynn 1965). Iguanids, agamids and chamaeleonids display ritualistically in species-specific patterns, which are a type of aggression and the chief determinants of social structure. Such display apparently functions in territorial declaration, which is a type of space dominance. Territoriality decreases intraspecific stress by stabilizing the social organization of the population and dispersing the species population, especially the males throughout the available suitable habitat (Carpenter 1967).

DISPLAY PATTERNS

Both sexes of *Agama atra* and *Cordylus cordylus* display. A weak display is given in a sitting position with the front of the body raised. In *A. atra* intense displays are given with the body raised on all fours and with most of the tail held off the ground. Two display types can be recognized. Courtship display consists of three sharply peaking high-level bobs each lasting about 1,2 seconds, followed by two very low-level bobs, each lasting about 0,5 of a second. The entire set takes about 4,0 seconds. Two or three such sets are normally delivered, with an interval of 2,0 to 6,0 seconds between each. The female responds to the male's display by presenting to him in a manner facilitating copulation, and some females seem to instigate it. Territorial display consists of two steeply peaking high-level bobs, as in courtship display, followed by two different bobs executed from the intermediate to the high-level range. The first of these lasts about 0,7 of a second, and the last for almost a second.

Courting and territorial display of *Cordylus cordylus* consists of a set of three intermediate-level bobs, each of 1 second duration. However, the delivery and body positioning determines whether the bob is for territorial or courting. In territorial display the defender, from its vantage point, delivers head down to the transgressor. The hind quarters are held to the substrate, but the fore part of the body is alternately raised and lowered, thus giving the delivery the appearance of 'push-ups'. While *Agama* display also can resemble 'push-ups', it is not so pronounced as with *Cordylus*. Three to four sets are normally given with a 5-second interval between each, though intensity depends on how deeply the intruder has violated the territory of the defender. In courting the display is given by both sexes facing each other laterally with the entire body and usually the tail held free of the substrate. During such display both sexes may feign biting the other before copulation commences and the number of sets given and the interval between each varies with the energy of individual pairs.

SOCIAL INTERACTIONS

On the coastal cliffs and inland rocky outcrops, *Cordylus cordylus* and *Agama atra* display is entirely intraspecific, and a *C. cordylus* territory may 'include' partly or wholly that of an *Agama*, even a despot. However, on the isolated rocky situations in sandy areas, only geckos apparently co-inhabit with

C. cordylus. It is difficult to know why *Agama*, and for that matter other lizards, seem absent. It is possible that other lizards have not been able to cross the sandy expanses to populate the rocky areas, but then *C. cordylus* with its preference for rocks would seem as effectively excluded from this habitat as *A. atra* and other lizards. Perhaps the high density of *C. cordylus* in such situations has effectively precluded the occupation of it by other saxicolous lizards.

A. atra females of one male's group seldom engaged in territorial disputes with each other, but frequently did so with females and occasionally even males of other groups. However, it is the prime responsibility of each male to maintain the territorial integrity of his group. When two females of different groups had a border dispute the respective males charged down, and if both males stayed on their own territories, the dispute was quelled. If, however, one or both males strayed over the border, much frenzied displaying resulted and on rare occasions vicious 'free-for-all' fighting. Incursions by members of despot groups are tolerated by non-despots, though their incursions are initially weakly challenged, followed by a submissive posture. The integrity of the retreat of any individual group is, however, viciously defended from but usually respected by an intruding despot group member. Despot group members were involved in fewer disputes, proportionately, among themselves than were non-despots.

The observed social interactions of 57 groups were studied in detail and are given in Table 5. While most matings are intra-group, despot males occasionally courted females of surrounding non-despot males. Mating between despot and non-despot group members occurred rarely, usually involving subdominant despot females and non-despot males, when the despot male was not looking.

Both sexes of *Cordylus cordylus* on coastal cliffs and on inland rock outcrops maintain individually discrete territories, though those of males are larger and overlap those of the females. There is no group formation as is the case of the agamids. Thus, both sexes defend their territories against and by cordylids of either sex. During the reproductive season, while challenging intruding members of the other sex, each sex is more tolerant of such intrusion. On the other hand, they defend more aggressively against members of their own sex.

C. cordylus occurs in groups on isolated koppies and scattered rocks in sandy areas. In those maintaining only home ranges, there is a definite home range, and each group tolerates transient incursion by the surrounding groups. It should be noted that such incursions were observed only very rarely. Each group's retreat is, however, strongly defended. In those groups with a territory and home range a group would tolerate incursion of the area called home range, but not the territory.

Those maintaining territories, with or without home ranges, would brook no incursion of their territories. Both adult males and females defend singly or together, occasionally with some assistance from the juveniles, particularly the older ones.

Display patterns and social structure of lizards are amply reviewed by

Table 5

Observed social interactions in a set of 51 *Agama atra* groups along the coastal cliffs at De Kelders, Cape.

TERRITORIAL CHALLENGES MATING

	Non-despots vs Non-despots N of Non-despot groups = 41			*Despots vs Non-despots*					*Despots vs Despots N of Despot Groups* = 10							
	♂♂ vs ♂♂	♀♀ vs ♂♂	♀♀ vs ♀♀	♀♀ vs ♂♂	♂♂ vs ♀♀	♂♂ vs ♂♂	♀♀ vs ♀♀	♀♀ vs ♂♂	♂♂ vs ♀♀	♂♂ vs ♂♂	♀♀ vs ♀♀	♀♀ vs ♂♂	*Intra*	*Inter*	*Intra*	*Inter*
Dec.	0	92	172	79	0	12	15	1	2	16	8	7	79	1	179	0
Jan.	17	77	100	60	10	5	7	2	4	7	2	0	28	0	78	0
Feb.	0	28	83	0	0	6	7	3	0	15	3	0	4	0	23	1
Mar.	0	30	33	20	1	2	3	9	0	12	7	10	0	1	10	0
April	10	10	51	14	5	2	4	8	0	14	8	7	0	0	0	0
May	0	5	0	0	2	0	0	0	0	0	0	0	0	0	0	0
June	2	10	20	2	4	7	5	0	0	4	4	0	0	0	0	0
July	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0
Aug.	3	15	4	4	6	8	0	0	6	5	1	0	0	0	0	0
Sept.	14	32	30	2	9	9	4	3	4	10	4	0	0	0	0	0
Oct.	20	40	62	23	5	17	9	5	7	11	7	3	50	0	112	0
Nov.	13	83	80	50	10	22	11	0	5	17	5	0	110	10	240	4

Carpenter (1962, 1967), Evans (1951), Hunsaker (1962), Hunsaker & Burrage (1969), and Ruibal (1967), and are virtually limited to American iguanids, though there have been some studies on agamids (Carpenter unpubl.; Cowles 1956; Greenberg 1957; Hairston 1957; Harris 1964; Mayhew 1963; Schmidt 1935). It appears that display patterns and social organization are similar between agamids, and their close relatives the iguanids. Chamaeleonid—an Ascalabotan family more closely related to the agamids—display has been studied by Brain (1961), Burrage (1973), Bustard (1958, 1965, 1966, 1967), Schmidt & Inger (1965), Spence (1966) and Von Frisch (1962).

For territorial, social and spatial behaviour, Carpenter (1967) differentiates between 'assertion display' and 'full or challenge display'. The former is a 'showing the flag', a weak or low intensity performance warning other lizards to 'keep their distance'. The challenge display is a high-intensity performance by very aggressive adults. As Carpenter observes, even freshly hatched and new-born young execute head-bobs and push-ups and I have discussed this on pages 13–16.

The following terms are applied by Carpenter to lizard behaviour patterns: individual space, territory, despotism, hierarchy, activity range (home range), and various levels of social organization, noting that those iguanids with the most elaborate aggression displays have the most complex social organizations. As Carpenter uses the term, social organization '. . . results from the interactions of members of the same species which influence or tend to establish patterns of space occupancy and inter-individual response'. These patterns may be rigid or transient; can seasonally vary.

Lizard display is considered to be intraspecific, but most lizards deliver at least the assertion display to all intruders. Depending on highly competitive areas and very critical resources, the more aggressive challenge display is only intraspecific. Courtship display favours a response only from members of the same species, especially of the opposite sex, for which Noble & Bradley (1933) consider it selects.

Fighting in wild populations of lizards is rare, but has been recorded for the iguanids *Sceloporus grammicus* (Evans 1946) and *Uta stansburiana* (Burrage 1966; Tinkle 1967). Some aspects of social behaviour may be different in captivity, with an increase or decrease in antagonistic behaviour (Burrage 1973, as regards chamaeleons). In a multi-species assemblage of captive iguanids, Hunsaker & Burrage (1969) found a shift from territories to a social hierarchy, with a development of despotism, as a result of population pressure and reduction of the available area; which hierarchy is established by increasingly vicious fighting, rather than the normal displays, as population pressure increases, and/or the available area is reduced. Similar social hierarchies, dominated by a despot male, have been recorded by Evans (1951) in wild populations of the normally territorial *Ctenosaura pectinata*, where the population was crowded around a rich source of food. They were crowded because their natural habitat had been burnt over. Their adaptation to living close to the food supply involved a reduction of available space for refuge and basking and a subsequent shift from the territorial system. Burrage (1966) in California, Ferguson (pers. commun.) in Colorado, and Knowlton *et al.* (1942) in Nevada, noted a somewhat similar arrangement in inland situations with a high *Uta stansburiana* population density and/or small area, whereby this normally territorial species merely defended only the burrow and had a small home range. Soulè (1964) noted this same phenomenon in high density insular and littoral populations of *Uta*, as Burrage (1966) also observed. Burrage (1966) notes that strand-dwelling *U. s. hesperis* possesses hotly defended territories on the backshore and home ranges seawards to at least the mean high tide limit. Clarke (1965) studied several iguanids, demonstrating a formation of dominant-subdominant hierarchies. Harris (1964) gives a detailed account of social behaviour in *Agama agama*, also noting formation of social hierarchies in high population densities. Harris notes the establishment of territorial borders in this species (see remarks on the litigated area between *Cordylus* Groups 1 and 2 on page 6), where two males often fought over a path between their boundaries. Fighting decreased as the border became established and eventually display along the path replaced combat, with rarer attempts at violation. Establishment of social hierarchies in high population densities limits the frequency of antagonistic behaviour that would result in attempts at territory formation. Also, in high population densities, the territory size would be reduced and the increasing rate would be high, necessitating almost continual defence on the part of the respective defenders, with insufficient or no time for other activities. It seems, however, that on topographically varied areas territorial establishment and high population densities are possible (Burrage 1966, and pages 4–5).

As Carpenter (1967) notes, it appears that most iguanids are territorial, but details of territories are not known for the vast majority of these. The data suggest territorial formation in agamids and some chamaeleonids, but few of these groups, especially chamaeleons, have been studied to the degree that iguanids have.

Our knowledge of social behaviour in reptiles is poor, and sometimes confusing, which is perhaps a pity since we could then better understand social behaviour patterns in the higher vertebrates.

SUMMARY

The spatial and social organizations are described of *Agama atra* and *Cordylus cordylus cordylus* inhabiting coastal cliffs, inland rock outcrops and dune and sandy situations. A total of 1 030 *A. atra* and 1 459 *C. cordylus* were marked. The population of *A. atra* is denser along the coastal cliffs and least dense on inland rock outcrops. *A. atra* is absent in suitable habitats surrounded by very dense scrub or large expanses of sand. *C. cordylus* occurs in all the habitats studied, as long as there are some rocks, which are the focal point of its activity and in which these lizards have their retreats. *C. cordylus* is densest

on the terraces of large rock koppies surrounded by sand and least dense in areas of isolated rocks among sand.

Territories and home ranges were computed only on the basis of 10 or more recaptures. *A. atra* only possesses territories. Adult population density varies inversely with territory size. Male territories are always the largest and contain several smaller female territories. The dominant female is always 'loyal' to the male. Towards the edge of the water there is a tendency to despotism, the territories of despots always being the largest. Juveniles are generally not challenged. Male juveniles leave the area they occupy as hatchlings, but females may remain. Despot groups were involved in proportionately less territorial challenges than non-despot groups. Male despots had more sexual contact with non-despot females than despot females had with non-despot males.

On the periphery of the larger koppies family groups of *C. cordylus* maintain a territory and a home range on the koppie itself. The larger the area and the lower the population density, the larger are the areas of the home range and the territories. In any situation and regardless of the spatial organization, the retreat burrow is defended. In sandy situations on isolated rocks only territorial organization occurs, with each territory being occupied by an adult male and female along with their juveniles of varied age groups. All members of each group defend the territory. The largest *Cordylus* territories occur on isolated rocks among sand. An experimental removal of a group of cordylids is given, showing territorial adjustments over a long period. Juvenile cordylids quit or are evicted from the territory of the 'family group' as they mature, or in the event of the death of their parents succeed to the adults' territory.

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WITH SOME ECOLOGICAL NOTES ON THE HABITS OF THE SPECIES

By

A. J. HESSE

Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R2,10

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1974

ISBN 0 949940 52 6

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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(With 1 figure)

[*MS. accepted 8 October 1973*]

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INTRODUCTION

Since the publication of my paper (Hesse 1972) on new Mydaidae from the Namib Desert and south-western Africa a new representative of the genus *Namibimydas*, described therein, was obtained from the west coastal region of South Africa.

As the genus *Namibimydas* is remarkable in many respects and as another representative of it has now been discovered far south of the Namib Desert, but also along the sandy coastal belt, a description of this new species is imperative.

This discovery of another species, represented by several specimens of both sexes, also enables me to supplement the original description of the genus which was based on only two old, somewhat damaged, specimens in the Stuttgart Museum.

Moreover the discoverer of the interesting new species also made some field observations on the habits of this mydaid which are as remarkable as the insects themselves and which, in view of our extreme ignorance of the ecology of Mydaidae, deserve to be recorded.

It all began early in January 1973 when Mr A. J. Prins, our Assistant Entomologist, was on vacation at Paternoster on the west coast between Saldanha Bay and Stompneus Bay and, when unprepared for the occasion, he first noticed a ♀ of these mydaids ovipositing in the sand.

To obtain specimens for the Museum Mr Prins, accompanied by Mr V.

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Branco, our artist, visited the same locality again early in February 1973. As in the case of most South African species and the Mydaidae in general, they also found that the desired insects were by no means plentiful and they were able to obtain only 8 specimens during the two days they spent there.

DESCRIPTION

Subfamily **Syllegomydainae**

Tribe Halterorchini

Genus *Namibimydas* Hesse

Namibimydas prinsi sp. nov.

This new species which I have great pleasure in dedicating to Mr A. J. Prins, who first discovered it, is characterized as follows:

Body-colour with the head and body mainly dark or blackish, appearing darker or more black in ♂♂, sometimes more greyish black in ♀♀; pleural and sternal parts and venter in some ♀♀ (tenerals) appearing pallid; sides of mesonotum, postalar calli, scutellum and metanotum in some ♀♀ (probably teneral) also sometimes paler, more obscurely pallid to dirty yellowish; lower part of buccal cavity (more extensive in ♀♀), anterior spiracles and notopleural suture, sclerites below wing-bases, posterior thoracic spiracles or part below halteres, hind margins of tergites 3–7 in ♂♂ and 2–7 in ♀♀, especially on sides, the sides of tergites obscurely in teneral ♀♀, lateral and posterior margins of hypopygial tergite 9 of ♂♂, processes and broad sides of navicular sternite 9 in ♂♂, and the acanthophorites and spines in ♀♀ yellow or yellowish; bullae, even in ♂♂, rather small, dull blackish red to black, elongate-oval, far apart along hind margins of tergite 2, very much smaller in ♀♀; antennae mainly dark blackish brown to black, only the articulations between the joints and the terminal tubercles usually paler, more pallid or yellowish (the entire antennae in teneral ♀♀ appearing subpallid or dirty yellowish); proboscis blackish brown to black, paler in tenerals; legs in ♂♂ with the coxae blackish brown to black, the middle and hind ones, especially latter, more yellowish brown towards apex below, the front femora mainly blackish brown, only the lower apical half yellowish, the middle and hind femora blackish brown above, yellowish below, the bases of hind ones also tending to be more yellow, with all the tibiae narrowly darkened above to a variable extent, the hind ones more evidently so apically, the tarsi mainly yellowish, but also slightly darkened above on apical parts of the joints, the last 2 or 3 joints sometimes more extensively darkened, the claws black in apical halves; legs in ♀♀ more extensively pallid or yellowish, more indistinctly or scarcely darkened on femora and tibiae above, the legs entirely pallid or yellowish in teneral forms.

Integument of head and body mainly dull, covered with greyish white tomentum to a variable extent; part of median ocellar ridge, antennal joint 3, head below on each side of buccal cavity, and the proboscis more or less shining;

thorax above mainly dull, leathery, with setiferous puncturation; pleurae also mainly dull, the middle part of sternopleuron, not covered with tomentum, shining to a variable extent; metanotum dull, leathery; abdomen dull above, setiferously punctured, the minute punctures lodging the hairs, the extreme sides of tergites tending to be more shiny, especially in ♀♀; the sides of tergites 2–7 in ♀♀, especially intramarginally, rugose, transversely striate in ♂♂, tergite 7 in ♀♀ transversely coarsely striated or grooved discally, and to a certain extent also on tergite 6 laterally and posteriorly; hood-like tergite 8 in ♀♀ punctured, less coarsely transversely striate, also more shining; sternum shining; venter in both sexes shining or subshining, transversely striated in ♀♀, less distinctly so in ♂♂; hypopygium in ♂♂ mainly dull, but basal junction between tergite and sternite 9, to a certain extent sides of 9, and keel of 9 shining; acanthophorites and their spines in ♀♀ also shining; legs, including coxae, more or less shining, the femora finely transversely striate, and the coxa, also more or less striate laterally.

Vestiture on head, body and legs mainly snow white in both sexes, longer and denser in ♂♂ than in ♀♀; that on head long, dense and conspicuous in ♂♂, slightly shorter in ♀♀; postvertical bristles white, slender, hair-like, difficult to see among the dense occipital hairs, more discernible in ♀♀; hairs on occipital part laterally behind eyes shorter than rest of cephalic hairs, shorter in ♀♀; palps with a tuft of long hairs and base of proboscis below also with some long hairs; head in front and sides of occiput dull, covered with fine greyish tomentum, denser and more evident along eye-margins; hairs on thorax above in front longer and denser than on rest of thorax, shorter in ♀♀; those on disc of mesonotum shorter and sparser, shorter in ♀♀, leaving a bare streak on each side in posterior half in both sexes, with a tuft of longish hairs medially in front of scutellum, and also with longish ones along notopleural part, above wing-bases, and on postalar calli; metanotum mainly bare on greater middle part, but with long hairs on sides; pleurae thinly covered with greyish tomentum, dull, except for the more shiny sutural and sternopleural parts, with an upper posterior tuft of long hairs on mesopleuron, long hairs along its posterior margin, long ones on pteropleuron and dense ones on metapleuron anterior to halteres and posterior thoracic spiracles, the hypopleuron mostly bare except for some long hairs along its posterior coxal border; abdomen in ♂♂ with fairly dense and long snow white hairs, those on tergites 1 and 2, especially on sides, slightly longer and denser, but those on sides of 3–5 in tufts, scarcely shorter, and those on sides of rest of tergites also long, but less in tufts, those on hypopygium, where present, also long and conspicuous, the hairs on venter in ♂♂ slightly sparser than on abdomen above, but also long, with the hairs on abdomen above in ♂♂, when viewed from above, more or less concentrated medially on tergites 3–7 in form of rosette-like tufts; hairs on abdomen above in ♀♀ long and dense only on tergite 1, especially on sides, with only a small tuft of shortish ones on sides of tergites 2 and 3, the rest of surface above on tergites 2–6 with minute, decumbent hairs in fine setiferous punctures and which in certain lights have a sericeous yellowish tint, with the hairs on tergite 7 and the posterior genital tergite 8 longer than the minute ones on preceding tergites, more sericeous white and directed forwards, with the abdomen above in ♀♀ also densely covered with greyish white or slaty grey tomentum on tergites 3–7 (this is sometimes denuded to a variable extent), the hairs on acanthophorites and anal lobes yellowish to golden yellowish, with the hairs on venter in ♀♀ minute, much sparser than on tergites, tinted slightly sericeous yellowish in certain lights, those on sternite 7 also sparser, but longer than on preceding sternites and directed forwards as on tergite 7; hairs on legs in ♂♂, especially on femora, denser, longer and more bushy than in ♀♀ in which sex the longer ones are distinctly less dense, especially on hind legs.

Head much broader than across broadest part of thorax, quite 3,8–4 mm in ♂♂ and 3,68–4,04 mm in ♀♀, though on the whole the head of ♀♀ appears relatively narrower; interocular space on vertex markedly broad as originally described for the genus, on the average slightly narrower in ♂♂ (2,32–2,68 mm) than in ♀♀ (2,4–2,72 mm), vertex not much sunk in, the central ocellar ridge also ends on vertex in a fairly deep sulcus as described for the type-species of the genus, the boss-like part on each side however less conspicuously prominent; antennae (cf. Fig. 1A) distinctly much shorter than interocular space, joint 1 thickened, about $1\frac{1}{2}$ to nearly 3 times length of 2, joint 3 stout, columnar, about, to even slightly more than, twice length of 1 and 2 combined, much shorter than club, its apical part broadened, the club itself nearly or about $1\frac{1}{2}$ times as long as joint 3, subspindle-shaped, especially in side view, thickest just before to about the middle, covered with a faint, but distinct, brassy pruinescence or tomentum, except on sensory area, with a belt of minute, spine-like hairs around the thickest middle part and across this part also a few longer, gleaming hairs mainly across the inner, upper and outer sides, especially in ♀♀, with the distinctly-demarcated sensory area, in more or less apical half below, large, elongate-ovate and bordered, ending apically in the crater-like terminal prominence lodging a minute stylet; proboscis (Fig. 1B) relatively long, slender, somewhat variable in length, about 2–2,6 mm (the latter when fully extended), on the whole slightly shorter than antennae, with a few, scarcely discernible, hairs along lower part on each side, at least in ♀, its labella short, oval, the apex bluntly rounded, sometimes appearing obliquely subtruncated; palps small, subglobular.

Wings comparatively short, not reaching tip of abdomen, entirely and markedly transparent, with a faint milky white tint in certain lights; veins white and transparent, only the extreme base of wings, costal vein and to a certain extent second vein slightly yellowish; venation like that of *Afroleptomydas*; first posterior cell obtusangular apically, either angular and shortly stalked apically or narrowly opening apically on second vein; second submarginal cell with an appendix basally; discoidal cell acute and shortly stalked apically; axillary lobe and alula moderately developed; halteres whitish.

Legs rather short, slender, the femora in ♂♂ slightly thicker than in ♀♀, the hind ones in ♀♀ longer, but in ♂♂ very slightly more thickened, the legs in ♂♂ distinctly more densely hairy; femora in ♂♂ with only dense long and short hairs below, no distinct spines being discernible, even on hind ones below; femora in ♀♀ also with long and short hairs, more above than below, but much fewer and less dense than in ♂♂, the front and middle ones without any detectable spines below, the hind ones less hairy, mainly short-haired above, with comparatively only a few long ones basally above and, in addition to a row of long bristly hairs along inner side below, with more or less two irregular rows of comparatively short, slender, white, bristle-like spines, as well as irregularly disposed, shorter, spine-like setae or seta-like spinelets below; tibiae curved in both sexes, the hind ones so near apex, hairy in both sexes, but more densely and to a certain extent longer so in ♂♂, especially the hind ones in latter sex with dense long and shorter hairs, with the front and middle tibiae in ♂♂ armed below with fine hair-like or bristle-like spicules, these in ♀♀ very slightly thicker, and hind tibiae in ♀♀ with stouter and more distinct spicules; apical spicules or spurs of tibiae below well developed, fairly long, golden yellow, equally developed in both sexes; tarsi with the spicules below, especially on hind ones, also well developed and golden yellow; claws in ♂♂ longer, more developed than in ♀♀; pulvilli in ♀♀ shorter and less developed than in ♂♂.

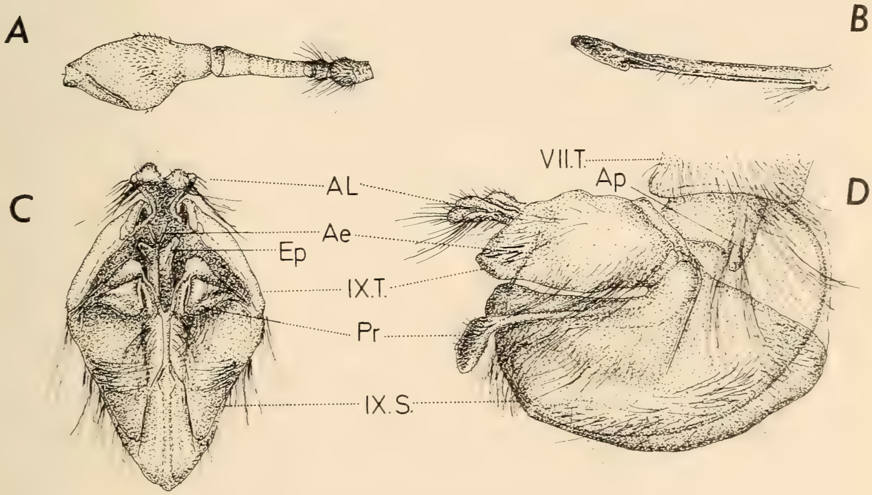

Fig. 1. *Namibimydas prinsi* sp. nov.

A. Side view of left antenna of ♀ allotype. B. Side view of proboscis of ♀ allotype. C. Posterior view of hypopygium of ♂ (vestiture partially omitted to show some structures more clearly). D. Right side view of the partially extruded hypopygium of a ♂. (AE = the characteristically long, curved aedeagus lodged in the keel part of sternite 9; AL = anal lobes; Ap = appendage of concealed or semi-concealed segment 8; Ep = epimere; IX.S. = large boat- or shell-shaped stermite 9; IX.T. = lid-like tergite 9, immovably attached to sternite 9; Pr = processes of sternite 9; VII.T. = tergite 7 partially or entirely covering tergite 8.)

Hypopygial complex of ♂ (Fig. 1C–D) with tergite 8 sometimes exposed as a short half-moon-shaped posterior part, depending on the upward or downward movements of the hypopygium, its projecting lateral lobe on each side of base of sternite 9 lobe-like; sternite 7 with only its hindermost part exposed, being almost entirely pushed forwards by base of sternite 9, its exposure or concealment being due to the upward, downward and forward movements of the hypopygium; hypopygium itself large and conspicuous as described for the genus (Hesse 1972; 160), in form of an oval box-like structure in side view, tergite 9 and anal lobes constituting a sort of fixed lid, the tergite itself about 1,6–1,8 mm long, convex, deeply and angularly incised posteriorly in which the anal lobes are situated, basally slightly transversely depressed above and on sides basally firmly and immovably united by a shining, weal-like, strongly-chitinized connection on each side dorsally to sternite 9, and which also constitutes the base of the prong on each side of the latter sternite; sternite 9 large, navicular, about 2,72–2,8 mm long, compressed from side to side, the more strongly-chitinized keel of the 'boat' being narrower than the sides above, posteriorly the sternite is deeply and angularly incised V-like; upper chitinized and ridge-like side or 'gunwale' of this boat-like sternite is continued posteriorly as a lateral flange to form the posteriorly projecting, flattened, downwardly-directed, tongue-shaped process or prong on each side, the upper posterior part of the 'gunwale', which also constitutes the upper part or corner of the V-shaped incision on each side, is prominent, rounded, strongly chitinized, shiny, and connected with the lateral prong, the less chitinized, paler sides of the sternite with long white hairs which are directed downwards posteriorly on each side of incised part; keel of sternite 9 is flattened, strongly chitinized, brown, and lodges the long, double-tubular aedeagus; aedeagus itself remarkably long, in form of a long, curved, double-tubular organ, composed of two parallel adherent tubes, thicker basally than posteriorly and lodged in the keel-part of sternite 9, bending forwards posteriorly just inside the posterior V-shaped incised part of the sternite and there becoming separated as two separate, thinner, aedeagal branches, each ending in a gonopore; epimere, as far as this can be seen, in form of a flattened bluntly-forked or bifid structure anterior to the aedeagal branches of aedeagus and pointing slightly backwards.

The process of copulation, though not observed by the collectors, probably takes place end to end as in Asilidae. In this case both the aedeagal tubes and the forked epimere are probably pushed backwards or posteriorly through the posterior V-shaped incision of sternite 9 to engage the genital organs of the ♀ in which they are also aided by the posterior lateral processes of the sternite which probably act as hooking structures.

Genital segments of ♀ structurally more or less as described and figured for the genus (Hesse 1972: 161, 164); hood-like tergite 8 with its hind margin slightly produced medially, there rounded and carinate, the disc transversely coarsely striate and punctured, more coarsely punctured intramarginally posteriorly; acanthophorites each with about 7 flattened, apically slightly broadened, yellowish spines, the first one at the base being more slender and rod-like; anal lobes with dense, short, stiff hairs or setae; sternite 8 half hidden, its hind margin emarginate or indented and its sides slightly rugose.

From 1 ♂ holotype, 1 ♀ allotype, 3 ♂ paratypes and 3 ♀ paratypes in the South African Museum.

Distribution

South-western Cape: Paternoster (A. J. Prins, 13 February 1973) (♂ holotype, ♀ allotype, ♀ paratype, and 3 ♂ paratypes); Paternoster (V. Branco, 13 February 1973) (2 ♀ paratypes).

Compared with the type-species *gaerdesi* Hesse (Hesse 1972: 161) from the Namib Desert, this new species may at once be distinguished by its much smaller size, relatively shorter, more slender legs, comparatively denser and entirely white vestiture in ♂♂, distinctly very much shorter or minute hairs on abdomen above in ♀♀, hairs on metanotum confined to sides, joint 3 of antennae proportionally longer relative to the other joints, much shorter and relatively less slender proboscis which is slightly shorter, not longer, than antennae and with a more bluntly-rounded apex of labella, the finer and more numerous spines and spinelets on hind femora below, especially in ♀♀, comparatively shorter apical spurs on tibiae, the more boat-shaped, not *Argonauta*-shell-shaped, sternite 9 of the ♂ hypopygium, the broader, more lobe-shaped lateral appendages of the half-concealed tergite 8, the more rounded upper corners of posterior V-shaped incision of sternite 9 which is not fused with lower part of posterior lateral lobes of tergite 9, the fewer (only about 6 or 7, not 8) spines on acanthophorites of ♀♀, and the less sharply or deeply indented hind margin of the half-concealed sternite 8 in ♀♀.

ECOLOGICAL NOTES

Habitat

According to the observations of Mr Prins this mydaid is by no means plentiful and occurs only along the littoral sandy zone on the coast near the sea, and is practically confined to the superlittoral part of it not reached by high tide. The region frequented is between the limit of the vegetation and the high tide mark, a white sandy environment strewn with broken shells, fragments of seaweed, especially those of *Ecklonia*, and also other debris washed up by the high tide or blown there by wind.

To this type of environment the mydaid is eminently adapted procryptically. Its dense snow white vestiture, transparent wings, greyish tomentum, and bare blackish patches on the abdomen of the ♀♀, render the species almost invisible against the background, and more so if individuals rest on the sand.

Movement and flight

According to Mr Prins this insect appears to be remarkably agile in moving to and fro and sideways on the sand, being able to crawl backwards as easily as forwards. In flight it appears to be as agile and even faster, darting backwards, forwards and sideways, within limits, with equal ease. These movements render it a difficult insect to catch. Moreover it appears to be very sensitive to vibrations in the sand caused by approaching footsteps or the slightest thump on the sand.

Oviposition

By sheer coincidence Mr Prins observed the procedure adopted by the ♀ in the deposition of her eggs. During his first visit he was resting on the sand when, a little distance away from him, a ♀ alighted and began to insert the tip of her abdomen in the sand. This she wriggled in until the entire abdomen disappeared in the loose sand. Not content with the depth reached she wriggled still further in until the entire thorax, wings and legs disappeared. Eventually the only parts of her anatomy still exposed were the pair of protruding antennae and front half of the eyes, frons, and clypeal part.

Equally rapidly she wriggled out of the sand again. Mr Prins then very carefully scooped out the patch of sand, containing some whitish eggs, and placed the sample in a glass tube with the intention of experimenting with it later on. Unfortunately some unauthorized visitor at the hotel, who wanted a glass tube for some other purpose, threw the sand away. Since then and during subsequent visits to the same area all efforts on the part of Mr Prins to observe another ovipositing female and to collect her eggs have been in vain.

As far as I am aware this is the first record of a dipterous insect ovipositing in this remarkable way of penetrating and almost disappearing backwards into a sandy medium. This method of oviposition appears to be still another adaptive response of this mydaid to a loose sandy environment.

Enemies

It was observed that a great enemy of this mydaid is a sand-loving and dune-frequenting species of lizard which, according to the two collectors, snapped up several specimens which they themselves tried to obtain.

SUPPLEMENTARY NOTES TO ORIGINAL GENERIC DESCRIPTION

As the original generic description of *Namibimydas* (Hesse 1972: 158–161) was based on only two old specimens (♂ and ♀) of the type-species *gaerdesi*, the addition of 8 specimens of the new representative of the same genus enables me to supplement, redefine or correct the original description of some of its structures as follows:

Head with the broad interocular space on vertex proportionally either more or less equally broad in both sexes or slightly broader in ♀♀ than in ♂♂; club of antennae longer than joint 3, elongate pyriform to spindle-shaped; the labella of the elongate and slender proboscis either spear-blade- or lance-blade-shaped and sharply pointed or subtruncately rounded apically.

Abdomen with tergite 8 in ♂♂ either entirely concealed or only partly exposed above base of tergite 9, saddle-shaped; sternite 7 in ♂♂ either displaced forwards and hidden under 6 or its posterior part exposed as a short cover over extreme base of sternite 9.

Hypopygium of ♂♂ remarkably and conspicuously large, in form of an oval, box-like structure, with tergite 9 and anal lobes constituting the lid, but the tergite itself immovably united on each side basally to sternite 9; latter sternite enormously developed and also as described for this species, boat-like, shell-like, keeled below, with a projecting process or prong on each side postero-dorsally, posteriorly vertically deeply incised (V-shaped), the upper angles or corners of the incision (or posterior angles of sides of sternite 9) prominent, rounded, or broadly projecting upwards under the apical part of posterior lateral lobes of lid-like tergite 9 (this latter condition described by me for the type-species *gaerdesi* (Hesse 1972: 162, fig. 6 right) as an obvolvent structure connected or fused to tergite 9 may probably not be united to tergite 9 at all, for it could not be seen as an unconnected structure in the old dried ♂ holotype); aedeagus (which also could not be seen properly in the unique ♂ of the type-species) is, as described for this new species, remarkably long, in form of a long, curved, strongly-chitinized, double-tubular organ, composed of two parallel, adherent tubes, lodged in the keel part of sternite 9 and which posteriorly become separated into two separate aedeagal branches which point forwards; epimere flattened and forked.

Legs with either a double row of distinct spines on slight tubercles, or with more numerous seta-like spinelets, on hind femora below.

DISTRIBUTION OF THE GENUS

In view of the fact that most of the known genera of Mydaidae in South Africa occur as separate, more or less geographically-restricted species and not as very widely distributed forms, the genus *Namibimydas*, which now occurs as two separate species, at Walvis Bay and Paternoster respectively, may also be represented by still other unrecorded species along the coastal, littoral, sandy belt, stretching from the south-western Cape to Angola. Judging from the habitat of the new species and that of the type-species it appears that this genus will be found to be restricted to the comparatively narrow, sandy or dune-sand environment along the west coast between the high tide mark and the landward limit of the non-marine vegetation.

SUMMARY

A new species *prinsi* of the genus *Namibimydas* Hesse, originally described from the Namib Desert, is described from Paternoster on the west coast between Saldanha Bay and Stompneus. Some ecological notes on the habits of the new species are added, and supplementary notes to the original generic description

are appended. A text-figure is given to illustrate the more important generic and specific characters of the new mydaid.

ACKNOWLEDGEMENTS

My thanks are due to the Assistant Entomologist Mr A. J. Prins and one of the Museum's artists, Mr V. Branco, who collected the specimens of the new species at Paternoster. To Mr Prins I am indebted for the interesting observations he made on the habits of this species.

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By

MICHAEL A. CLUVER

Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R3,80

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1974

ISBN 0 949940 53 4

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

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(With 6 figures)

[*MS. accepted 15 October 1973*]

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INTRODUCTION

The dicynodont *Myosaurus gracilis* Haughton is known from several small skulls, some with associated postcranial remains, all from a single locality on the commonage of Harrismith, O.F.S., South Africa, where the remains of a *Lystrosaurus* zone (Basal Triassic) fauna occur in abundance. The genus is remarkable in that, until recently (Hotton 1974), it represented the only small-sized dicynodont form known to have survived the Permian-Triassic transition as recorded in the South African Beaufort succession. With an average skull length of 40 mm, *Myosaurus* is dwarfed by other South African Triassic dicynodont genera, such as its contemporary *Lystrosaurus* (typical skull length 100 mm) and the *Cynognathus* zone *Kannemeyeria* (typical skull length 400 mm).

In view of its almost isolated stratigraphic position, the cranial morphology and possible relationships of *Myosaurus* would appear to be matters of some interest, but after Haughton's (1917) description, no further preparation of the South African Museum type material was undertaken, with the result that, with the exception of the skull roof and occiput, the skull structure remains largely unknown. With the emphasis in dicynodont classification now increasingly involving areas other than the skull roof (Toerien 1953; Cluver 1970; Hotton & Cluver in press) it seemed that a detailed description of the material, including the palate, basicranium, braincase and lower jaw, would be necessary before the relationships of the genus could be adequately considered.

Ann. S. Afr. Mus. **66** (4), 1974: 35–54, 6 figs.

In his original description, Haughton (1917) considered that *Myosaurus* was allied to *Emydops*, but differed in being free of molar or canine teeth; Van Hoepen (1934) came to a similar conclusion. Broom (1932) mentioned resemblances to *Cistecephalus*, from which, however, the genus differed in its small size and retention of the preparietal bone. The only other reference to the relationships of *Myosaurus* was made by Broom (1941) when describing *Myosauroides minnaari*, which he thought differed from *Myosaurus* mainly through its lack of a preparietal. *Myosauroides*, from the *Cistecephalus* zone, could, according to Broom, be placed '. . . somewhere between *Myosaurus* and *Cistecephalus*' (p. 210).

MATERIAL AND TECHNIQUES

In addition to the two co-type skulls (S.A.M. Nos 3526 and 3526a) in the South African Museum, five specimens were obtained on loan from the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; two of these latter specimens (B.P.I. Nos 2701b and 4269) have associated lower jaws. Disarticulated postcranial material is associated with the two type skulls, while B.P.I. No. 4269 has the articulated anterior third of the postcranial skeleton attached to the skull.

The bulk of the preparation was confined to the two type skulls, which are well preserved and virtually undistorted and which together complement each other to provide a complete picture of the skull morphology. These two specimens were completely cleared of matrix by means of automatic mallet and needle, and all areas, including the interior of the braincase, were made available for examination. Specimen 3526a had suffered a fracture across the back of the skull base during the original preparation, and it was thus also possible to clean out the inside of the left otic capsule. Preparation of the B.P.I. specimens was not carried to the same extent, and was mainly limited to exposure of the palate and, in two cases, the lower jaw.

Illustrations of the skull are orthoprojections; in the case of dorsal and ventral views the projections are on to a plane including the base of the foramen magnum and the ventral, inner surface of the nostril. The illustrations are mainly composite reconstructions of both co-type skulls, but, thanks to the almost total lack of distortion in the material, the reconstructions accurately represent the actual condition of the skulls.

In addition to these specimens of *Myosaurus*, the type (R.C. 54) of *Myosauroides minnaari* Broom was obtained on loan from the Rubidge Collection, and the palate and mandible prepared. A second, better preserved specimen of this species (A.M.N.H. 8209), loaned from the American Museum of Natural History, New York, yielded additional information after preparation. Several specimens of *Cistecephalus* in the collection of the South African Museum as well as the type and paratype (BMNH R4956, R4957) of *Emydops longus* in the British Museum (Natural History) London, were also used for comparison with both *Myosaurus* and *Myosauroides*.

CLASSIFICATION

For present purposes, the dicynodont classification of Haughton & Brink (1954), modified after Romer (1966) (see also Cluver 1974) can be most conveniently used to state the present systematic position of *Myosaurus gracilis*:

Class: Reptilia
Order: Therapsida
Suborder: Anomodontia (*sensu* Romer 1966)
Infraorder: Dicynodontia (*sensu* Romer 1966)
Family: Endothiodontidae (*sensu* Haughton & Brink 1954)
Subfamily: Pristerodontinae
Genus: *Myosaurus* Haughton

Diagnosis: Skull small, with relatively large orbits and weak snout. Intertemporal portion of skull roof wide. Postfrontals absent, pineal foramen relatively far back in skull roof. Squamosal flared sharply laterally above quadrate. Frontals and prefrontals make near-contact in midline ventrally to olfactory passage. Secondary palate long, no anterior palatal ridges. Palatine small, meeting premaxilla. Long vomerine septum dividing internal nares.

Myosaurus gracilis Haughton (1917)

Diagnosis: as for genus.

Co-types: Two skulls in nodule (S.A.M. Nos 3526 and 3526a) from Harrismith, O.F.S., South Africa.

Horizon/age: Lystrosaurus zone, Lower Triassic.

CRANIAL MORPHOLOGY OF *MYOSAURUS GRACILIS*

Skull roof

The nostrils are nearly terminal, and the anterior portion of the premaxilla, dividing the nostrils, is accordingly reduced to a delicate splint of bone, missing in most specimens. A short internasal process of the premaxilla extends back between the nasals, which may form slight bosses above and behind the nostrils. Behind the nostrils, and in front of the anterior border of the orbits, there is a slight narrowing or waisting of the snout, adding to the generally weak appearance of this anterior part of the skull. The septomaxilla is small, and confined to the interior of the nostril, where it forms part of the posterior wall. The maxilla rises fairly steeply behind the nostril, but is separated from the prefrontal by a narrow but persistent process of the lacrimal (Fig. 1B). The prefrontal is not strongly developed on the outer surface of the skull, and no boss is formed; the large orbit is thus almost circular in antero-lateral view.

The frontals (Fig. 1A) are important elements of the skull roof, meeting the nasals far forwards in an almost transverse suture, and extending back to a point level with the middle of the temporal fenestra. The pineal foramen lies

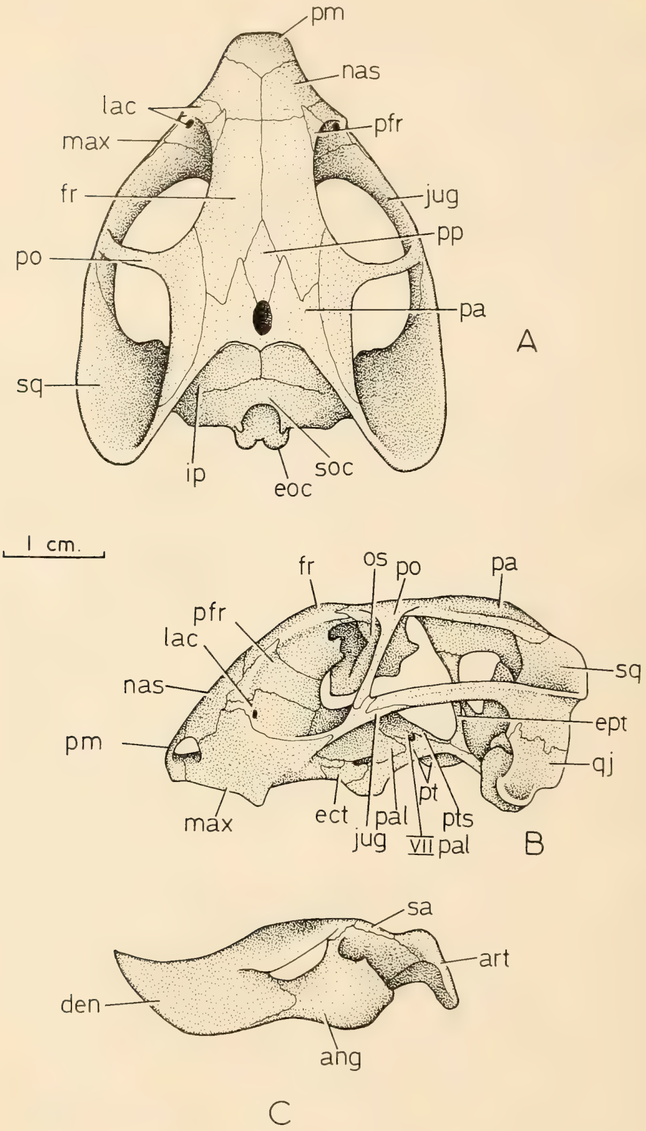

Fig. 1. *Myosaurus gracilis* × $\frac{3}{2}$. A–B. Skull in dorsal and lateral view respectively. C. Mandible in lateral view.

relatively far back in the skull, and there is a prominent, diamond-shaped preparietal.

Apart from the posterior portions of the frontals, the broad intertemporal region is composed of the parietals and postorbitals, a postfrontal being altogether absent (Fig. 1A). Each parietal is wide posteriorly, and bifurcates anteriorly to surround the rear of the frontal of its side. Laterally it meets the postorbital, which lies as a thin horizontal sheet over the upper part of the temporal opening. This part of the postorbital is essentially a lateral continuation of the parietal sheet, and therefore a bone of the dorsal skull roof. The lateral edge of the post-orbital is thickened and forms a stout dorsal border for the temporal fenestra.

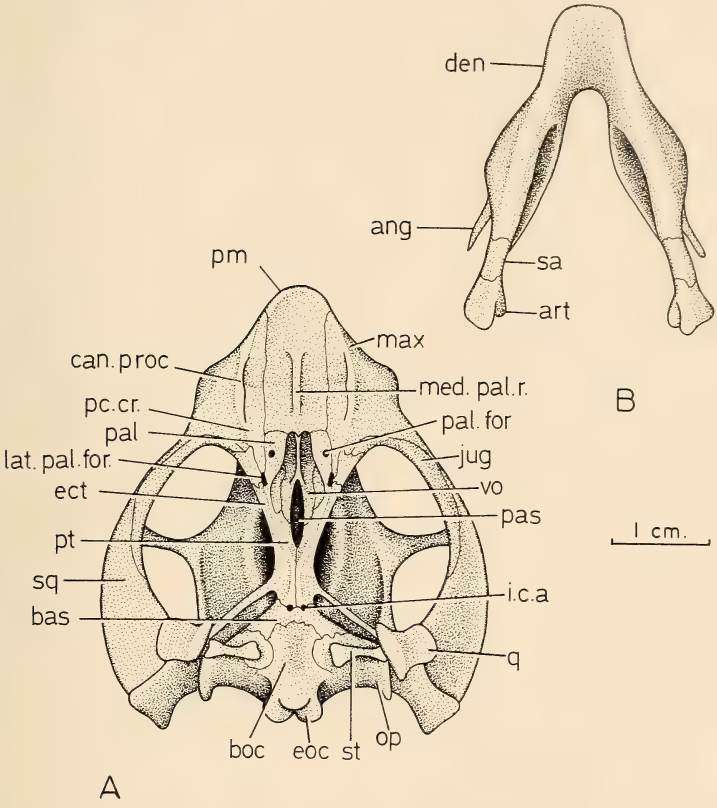

Fig. 2. *Myosaurus gracilis* × $\frac{3}{2}$. A. Skull in ventral view. B. Mandible in dorsal view.

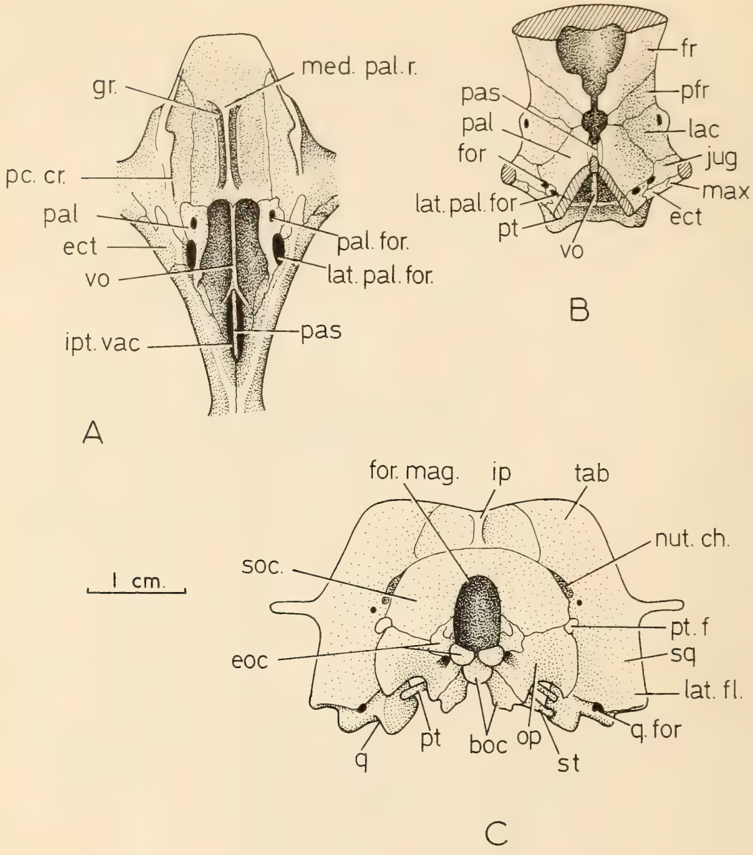

Fig. 3. *Myosaurus gracilis*. A. Palate in ventral view, × 2. B. Snout in posterior view, × $\frac{3}{2}$. C. Occiput, × $\frac{3}{2}$. Left stapes removed.

Occiput

The interparietal (Fig. 3C) lies wholly in the occiput, and does not overlap on to the skull roof, from which the occiput is clearly demarcated (Fig. 1A). A median crest divides the interparietal into two halves. Although not clear in all specimens, tabulars are present and lie as squarish plates on each side of the interparietal. The supraoccipital is clearly distinguishable from the surrounding dermal bones, and is on each side bounded by the crescent-shaped opening of a nutrient channel (Fig. 3C), similar to that found in *Lystrosaurus* (Cluver 1971). Each opening lies between the lateral edge of the supraoccipital and the medial edge of the squamosal and is closed off ventrally by a short inner lappet of the squamosal which makes a brief contact with the ventrolateral corner of the supraoccipital. This process of the squamosal is pierced by a small foramen, which opens into the crescent-shaped space; directly below lies the large posttemporal fenestra. It seems (Cox 1959; Cluver 1971) that all of these channels served for the forward drainage of blood from the neck musculature into the cranial cavity, prior to its discharge into the v. capitis lateralis and v. jugularis (see below).

The sutures between supraoccipital, exoccipital and opisthotic are clearly visible in occipital view. The exoccipital, carrying a process for articulation with the proatlas, is seen to have a limited lateral extent, so that the opisthotic meets the supraoccipital in a suture leading towards the posttemporal fenestra. The opisthotic is a stout bone, abutting against the squamosal laterally and notched for the passage of blood-vessels on the other three sides. Dorsally it closes off the posttemporal fenestra, through which passed the v. capitis dorsalis (Cox 1959); medially it forms the lateral wall of the jugular foramen and ventrally it is cut away for the course of the v. capitis lateralis.

The area of the braincase between the posttemporal fenestra and the jugular foramen is swollen, and stands out as a smooth bulge on the occiput. The exoccipitals meet in the midline ventrally, and form the posterior floor of the foramen magnum; the two exoccipital condyles overhang the basioccipital condyle to a quite considerable extent (Fig. 2A).

The squamosal forms the lateral border of the occipital plate in the usual way, but ventrolaterally it is drawn out as a prominent flange (Fig. 3C, lat. fl.) which extends out from directly above the quadrate. This is an unusual feature, not seen in other dicynodonts, and is most likely related to development of the lateral external jaw adductor muscle mass, for which the anterior face of this portion of the squamosal serves as an area of origin.

The quadrate (Figs 1B, 2A, 3C) is basically a vertical disc with a sharply offset lateral articular shelf, and the articular surfaces are at sharp angles to each other. The ventral, highly convex edge of the disc articulates with the medial articular process of the lower jaw, while the lateral, more gently convex lateral condyle meets the main articular surface of the articular bone. The two articular surfaces of the quadrate are separated by a sharply defined vertical step.

The quadratojugal is fused with the dorsal surface of the lateral quadrate condyle, and meets the squamosal dorsally in a highly interdigitating suture. A large quadrate foramen (Fig. 3C) lies between the quadratojugal and quadrate, and opens low down on the occiput between the rear of the lateral quadrate condyle and the ventral edge of the descending sheet of the squamosal.

The stapes (Fig. 2A) is a simple rod, inflated both proximally, to form a fairly distinct footplate, as well as distally, where it lies up against the inner side of the medial quadrate condyle.

Skull base and palate

In ventral view (Figs 2A, 3A), the skull displays several features of importance. The large fenestrae ovales are rimmed by the high, thin-walled basioccipital-basisphenoidal tubera. The porous nature of the bone surrounding each

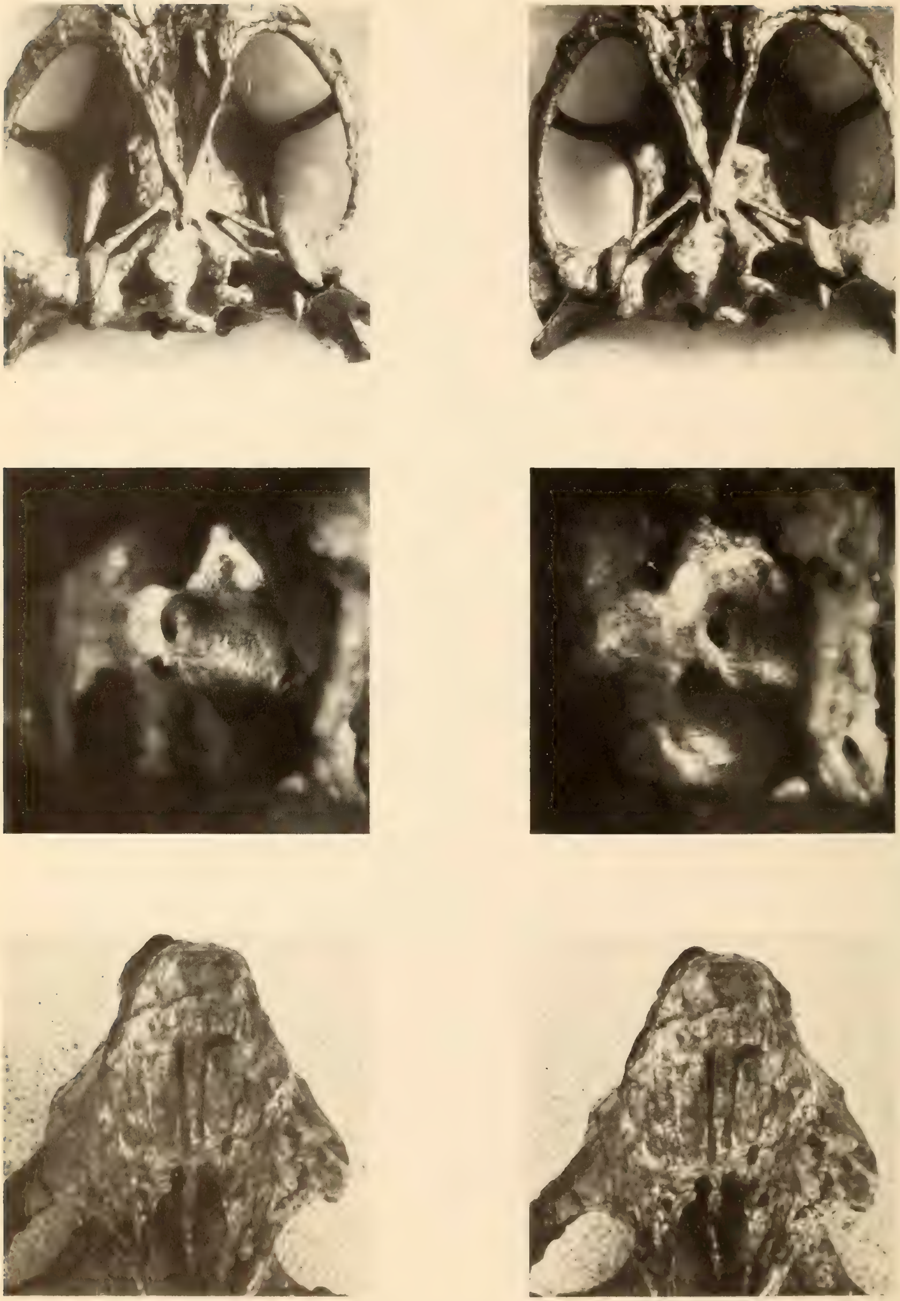

Fig. 4. *Myosaurus gracilis*. Stereophotographs of: A. Braincase in ventral view (S.A.M. No. 3526). B. Interior of braincase showing left prootic and floccular fossa (S.A.M. No. 3256a). C. Palate (S.A.M. No. 3526a).

fenestra suggests the former presence of cartilage, in which the functional fenestra ovalis probably lay.

The pterygoids meet in the midline beneath the basisphenoid, anterior to the foramina for the internal carotid arteries, and a fairly strong median crest is formed. The slender quadrate ramus of each pterygoid extends back and laterally, terminating in a recess in the medial surface of the quadrate of its side (Fig. 3C). In front of their meeting in the midline, the pterygoids diverge laterally and form the outer borders of the long, vaulted choana. Anteriorly they meet the ectopterygoids and palatines of each side and terminate as fairly prominent, vertically expanded blades. Between each anterior pterygoid blade and the palatine is a sizeable, slit-like lateral palatal foramen; a freestanding ventral process of the palatine forms a part of the medial border of this foramen.

The palatal portion of the palatine is limited to a small, thin sheet, perforated by a large foramen (Figs 2A, 3A, pal. for.). This foramen, unusual in dicynodonts, opens into the interior of the choana above the horizontal portion of the palatine, where a second foramen between the palatine, jugal and ectopterygoid leads into the antero-ventral corner of the orbit in front of the upper opening of the lateral palatal foramen (Fig. 3B, for.). The palatal surface of the palatine is smooth, and its generally delicate construction, coupled with its apparent association with a blood-vessel or nerve, makes it doubtful whether it supported a layer of horn, as in other dicynodonts. The significance of this is more fully discussed below.

In the roof of the choanal vault the ventral edge of the parasphenoidal rostrum is visible in the long and narrow interpterygoidal vacuity. The vacuity is bounded anteriorly by the vomers, in normal dicynodont fashion; in front of this the two halves of the vomer are fused into a thin vertical septum which extends forwards to meet the premaxilla and divide the anterior part of the choana into two passages.

The premaxilla forms most of the secondary palate. It meets the palatine posteriorly and the maxilla is confined to an altogether lateral position. Anterior palatal ridges are lacking, but a median premaxillary ridge is a distinct feature. In section the ridge is T-shaped, with an inflated palatal portion supported by a thin vertical girder. On each side of the girder and parallel with it, the premaxilla is drawn out as a longitudinal crest, so that the median ridge is in effect flanked by a pair of partially enclosed channels (Fig. 3A, gr.). Anteriorly, where the median ridge merges with the general palatal surface, the grooves appear to diverge laterally without, apparently, penetrating the premaxilla, while posteriorly they lead towards an anterior notch in the choana, between premaxilla, palatine and vomer.

Similar premaxillary grooves have been described in other dicynodonts and it has been suggested (Cluver 1971) that they marked the passage of nutrient blood-vessels and/or nerves. On the other hand, the anterior choanal notch of dicynodonts, which the grooves approach in *Myosaurus*, has been indicated as the most likely point of emergence of the duct of Jacobson's organ (Cluver 1971), and the condition in *Myosaurus* could perhaps be interpreted as indication of a doubling back, in an anterior direction, of the duct to an opening in the primitive forward position. Equally possible, however, is an association between the premaxillary grooves and the palatine foramina, and with the lack of conclusive evidence the question must remain unresolved.

The palate is bounded laterally and anteriorly by a modest rim, which is drawn down to a small but clear maxillary caniniform process. The medial surface of this rim has a shallow depression in front of the caniniform process, but this is not the deeply incised palatal notch of '*Dicynodon*' *testudirostris* (Cluver 1970; Hotton & Cluver in press), nor is any caniniform flange present. Between the rear of the caniniform process and the expanded pterygoidal sheet on the choanal border, the palatal rim is at first a fairly sharp postcaniniform crest, and then becomes a low and smoothly rounded ridge, formed by the maxilla and the small, tightly interdigitated ectopterygoid. As with the palatine, the palatal surface and rim is nearly devoid of nutritive foramina and channels, and the pitting and rugoseness of other dicynodont palates is absent.

Braincase, basicranial axis and orbit

The otic capsule is the most prominent part of the preserved bony braincase. The opisthotic and exoccipital portion is inflated posteriorly above the jugular foramen, as stated above, while in front the prootic is laterally displaced to accommodate what appears to have been a relatively large brain. That the structures of the brain were closely apposed to the walls of the braincase is further suggested by the presence of a very deep floccular (sub-arcuate) fossa in the rear of the prootic (Fig. 4B). This fossa is remarkable in that it communicates, by means of a fairly large opening, with the vestibule of the inner ear (see below). On its anterior, outer face the prootic is deeply incised between the posttemporal fenestra and the posterodorsal corner of the braincase, and below its meeting with the parietal the prootic is cut away to form a very distinct notch leading into the interior of the braincase. A very clearly demarcated channel for the v. capitis dorsalis (Cox 1959; Cluver 1971) is thus formed. As the posttemporal fenestra opens more or less directly into the ventral part of this passage, and as the prootic shows no comparable groove below the fenestra, it appears that most of the blood from the occiput passed into the v. cephalica posterior within the braincase (Dendy 1909; Swain 1968); a limited portion only would probably have flowed down through a sinus below the posttemporal fenestra to meet the v. capitis lateralis.

Within the braincase, the pair of posterior cephalic veins would have been joined by the small occipital veins passing forwards between the supraoccipital and interparietal (see above) before descending to issue from the skull as the jugular veins. There is a deep hollow in the inner surface of the parietal in the postero-dorsal corner of the braincase above the foramen magnum, and it seems likely that in life this was filled by a dorsal cartilaginous extension of the supraoccipital, similar to that of *Lystrosaurus* (Cluver 1971); the pair of occipital veins would probably have entered the cranial cavity at this level.

Several inner ear structures can be made out. The fenestra ovalis is relatively very large (Fig. 4A), but was probably furnished with a cartilaginous rim during life. From the fenestra ovalis a short, wide chamber leads to the vestibule. This chamber, which may be called the perilymphatic chamber, is medially expanded below the vestibule of the inner ear, and is unlike the simple auditory tube of other dicynodonts, which links the fenestra ovalis with the deep structures of the inner ear. It appears that in *Myosaurus* a fairly large footplate, perhaps partly cartilaginous, was associated with a considerably expanded perilymphatic sac or cistern. Inside the braincase the internal auditory meatus is confluent with the inner opening of the jugular canal, so that at this point the otic capsule is separated from the skull base by a wide space, leading to the jugular canal behind, the fenestra ovalis ventrally and the vestibule and sacculo-cochlear recess medially. A relatively large recess, which housed the ampullae of the horizontal and anterior vertical semicircular canals, is visible, and it appears that the utriculus lay in a dorsal cavity fairly clearly demarcated from the wider saccular space below.

The floccular fossa opens into the utricular cavity, as stated above. This appears to be a unique condition. Olson (1944) states that the anterior vertical semicircular canal was in many cases confluent with the floccular fossa in his sectioned dicynodonts, but in *Myosaurus* this is not the case, and the canal in question arises far forwards of the inner opening of the fossa. It seems very unlikely that a direct communication between the interior of the otic capsule and the cranial cavity ever existed, and capsule and fossa were almost certainly membraneously separated during life.

Close in front of the internal auditory meatus lies a foramen, in the position of the internal opening of the VIIth (facial) nerve (Olson 1944; Cluver 1971). A short and narrow canal leads into the foramen from the anterior, saccular part of the vestibule, below the anterior ampullary recess, so that there appears to be a connection between the otic capsule and the facial canal. Comparison with a *Lystrosaurus* braincase (S.A.M. No. 11180; see also Cluver 1971) shows that in this genus a deep and narrow cleft leads from below the front of the anterior ampullary recess to the region of the facial nerve foramen, while what appears to be a similar cleft can be seen in some of Olson's (1944) sectioned dicynodonts. Closure and canalization of such a cleft up to the level of the facial foramen would lead to a condition similar to that seen in *Myosaurus*, but the function of the cleft or canal remains obscure. While in a form such as *Lystrosaurus* the cleft could have supported a portion of the perilymphatic duct system, in *Myosaurus* the canal apparently enclosed a nerve, blood-vessel or duct, which then, presumably, either emerged into the anterior part of the braincase alongside the root of the facial nerve, or passed down the facial foramen to leave the braincase with the cranial nerve. Serial grinding of a *Myosaurus* braincase would seem to offer the only means of resolving the question.

No fenestra rotunda appears to have been present, and the perilymphatic duct probably terminated in the jugular foramen, as suggested by Olson (1944).

The floor of the braincase, formed by the basioccipital and basisphenoid, is smooth and flat, and a dorsum sellae is altogether absent. The paired internal carotid arteries enter the interior of the skull through a wide common opening, which probably housed a ventral part of the hypophysis as well. A true fossa hypophyseos is absent. Alongside this opening the ossified bases of the pilae antoticae of the prootics extend up as a pair of relatively long and stout pillars, inclined slightly forwards. Immediately lateral to each pillar lies the slender epipterygoid, rising from its footplate to meet a broad, descending flange of the parietal. This sheet of the parietal, together with the epipterygoid and ossified pila antotica, forms an incomplete sidewall to the brain cavity at the hypophysis-pineal organ level.

Immediately in front of the inner opening of the internal carotid artery lies a low bony septum, identified as a separate presphenoid element by Cluver (1971) but regarded as an anterior basisphenoidal extension by some authors (Broom 1926; Cox 1959). In *Myosaurus* the presphenoid (Figs 1B, 3B) is clasped by the trough-like cultriform process of the parasphenoid and, as shown in *Lystrosaurus* (Cluver 1971), was probably connected to a more extensive cartilaginous interorbital septum at its abrupt anterior truncation. Laterally and ventrally the parasphenoid is firmly held by the pterygoids up to the latter's meeting with the palatines. At this point a slit-like foramen is formed on each side between the pterygoid and the side of the parasphenoid-presphenoid septum (Fig. 1B, VII pal.), and presumably served for the exit of the ramus palatinus of the VIIth (facial) nerve.

Anterodorsally the neurocranium is represented by the ossified orbitosphenoid-mesethmoid complex (Fig. 1B, os). This complex is best seen in S.A.M. No. 3526a, where it has been displaced into a position suitable for detailed preparation. The orbitosphenoid is a wide trough, with a ventral notch posteriorly for the exit of the pair of optic nerves, and bears a prominent ventral keel which is deepest anteriorly. This part of the complex, lying up against the ventral surface of the frontals, presumably housed part of the olfactory lobes. The mesethmoid, a short but deep septum clearly distinguishable from the orbitosphenoid, divides the pair of olfactory channels as they pass forwards into the snout.

Only a short space separates the mesethmoid from the anterior, inner wall of the orbit. *Myosaurus* is unusual among dicynodonts in that the frontal, prefrontal and lacrimal, which normally surround a wide, anterior orbitonasal opening leading into the snout, have undergone an extensive medial development, the frontals in fact almost meeting in the midline below the olfactory opening (Fig. 3B). The interior of the snout is thus, with the exception of the olfactory opening, almost completely closed from the orbit; a small, almost circular space between the prefrontals probably represents an orbitonasal opening reduced from the usual dicynodont condition (see e.g. *Lystrosaurus*, Cluver 1971). Ventrally the palatines meet the prefrontals near the midline, thereby excluding the lacrimal from the border of the orbitonasal opening.

Below and behind the orbitonasal opening the palatines lie closely apposed to the parasphenoidal rostrum, so that the midline region is completely floored by bone.

Lower jaw

The symphyseal region, usually powerfully developed in dicynodonts, is relatively weak in *Myosaurus* (Figs 1C, 2B). There are no dentary tables and the very slightly concave dorsal dentary surface is scooped out in front to form a deep cleft behind the anterior shovel-shaped tip. This anterior edge is not well preserved in any specimen, but indications are that it was at least fairly sharp. The weak development of the dentaries is reflected in the considerable exposure of the splenials in anterior view.

A fairly prominent lateral dentary shelf is formed in front of and above the mandibular fenestra, while the rear half of the dentary's dorsal surface, behind the slightly grooved anterior portion, is narrow and smoothly rounded. The anterior surface of the dentary, below the shovel edge, is heavily pitted by nutritive foramina, and indications are that a horny sheath covered this front part of the lower jaw. No such pitting can be detected on the dorsal edges of the dentary, where clear evidence of a horn covering is usually found in dicynodonts.

The jaw is deepest in the angular region, even when the extensive reflected lamina of the angular is not taken into consideration. In the rear of the jaw the articular is seen to be drawn down ventrally into a long and powerful retro-articular process, but little else, especially of the inner surfaces, can be made out.

JAW FUNCTION IN *MYOSAURUS*

The jaw musculature of dicynodonts has been reconstructed by Crompton & Hotton (1967). From subsequent comparisons (Cluver 1970, 1971) it appears that the area of greatest variation in this system lies in the nature of the insertion of the external adductor muscles on the lower jaw. Two divisions of the external adductor musculature were present in dicynodonts, these being a medial external adductor arising from the bones surrounding the temporal fenestra, and a lateral external adductor arising from the anterior surface of the descending squamosal sheet and the ventral surface of the squamosal's zygomatic bar. Crompton & Hotton (1967) suggest that in dicynodonts such as *Lystrosaurus* and *Emydops* the medial mass inserted into a groove in the dorsal surface of the dentary behind the dentary tables, while the lateral mass was attached to a lateral dentary shelf lying above and partly in front of the mandibular fenestra. However, it appears that in certain genera (Cluver 1970, 1971) the groove and shelf are absent or present only in modified form, and it has been suggested (Cluver 1974) that an additional slip of the external adductor muscle inserted around the dorso-lateral margin of the adductor fossa, on the inner side of the jaw ramus.

In *Myosaurus* no dorsal dentary groove is found, but a prominent lateral dentary shelf is present, and the dentary is powerfully buttressed over the mandibular fenestra. The lateral external adductor muscle was therefore provided with a well-defined area of attachment, but the limits of the insertion area of the medial group are less clear; this muscle probably attached on the inner surface and the rounded dorsal edge of the dentary, behind its horn-covered anterior portion.

The possible range of jaw movements in small edentulous dicynodonts such as *Cistecephalus* have been recently discussed (Cluver 1974) and it has been shown that the typically wide cistecephalid palate, narrow symphyseal region and relatively flat quadrate and articular articulation surfaces could indicate lateral movement across the palate during the anteroposterior cycle of jaw movements as described in dicynodonts by Crompton & Hotton (1967). In this respect, however, *Myosaurus* appears to have retained the primitive range of movements: the articular surfaces of the quadrate are at sharp angles to each other and quadrate-articular rotation appears to have been highly unlikely. In addition, the long and narrow secondary palate, with rim and caniniform processes hardly wider than the symphyseal area of the lower jaw, suggests that upper and lower apposing surfaces would have met during strictly anteroposterior sliding movements.

The nature of these occluding surfaces, however, is unusual. As shown above, the dentaries are weakly developed anteriorly, and there are no dentary tables such as appose the palatine and maxilla in *Lystrosaurus* and *Dicynodon* (Cluver 1970, 1971). At the same time, a battery of mandibular teeth, which bite against the palatine in forms such as *Emydops*, is absent, and the apparent lack of a horn covering in the palatine region, as well as the delicate structure of that bone, appears to be a consequence of this.

The only clear evidence of horn is found on the anterior surface of the fused dentaries, and points to the presence of a horny sheath over the sharp-edged, square tip of the symphysis. Behind this the lateral edge of the dentary, bordering the slightly concave dorsal surface, is fairly sharp and may have carried a posterior extension of the beak. While the shovel-like tip would have acted against the anterior premaxillary surface, as suggested by the absence of anterior palatal ridges, the more lateral parts of the lower beak would have had some slicing effect against the palatal rim, which, in turn, was probably furnished with a corresponding horny layer. It seems unlikely, in view of the smooth bone surfaces involved, that either of these lateral horn coverings were substantial or extended as far medially as the median palatal ridge with its pair of flanking channels.

The dietary preferences of an animal such as *Myosaurus* can only be speculated upon. Certainly, the lack of well-developed shearing and crushing areas in the mouth suggests a food source very different to the presumably fairly coarse vegetation for which the contemporary *Lystrosaurus* was equipped. Cox (1972) has recently suggested that the small cistecephalid *Kawingasaurus* fed upon soft-bodied, and presumably slow-moving, invertebrates, and a roughly similar diet in the case of *Myosaurus* cannot be ruled out.

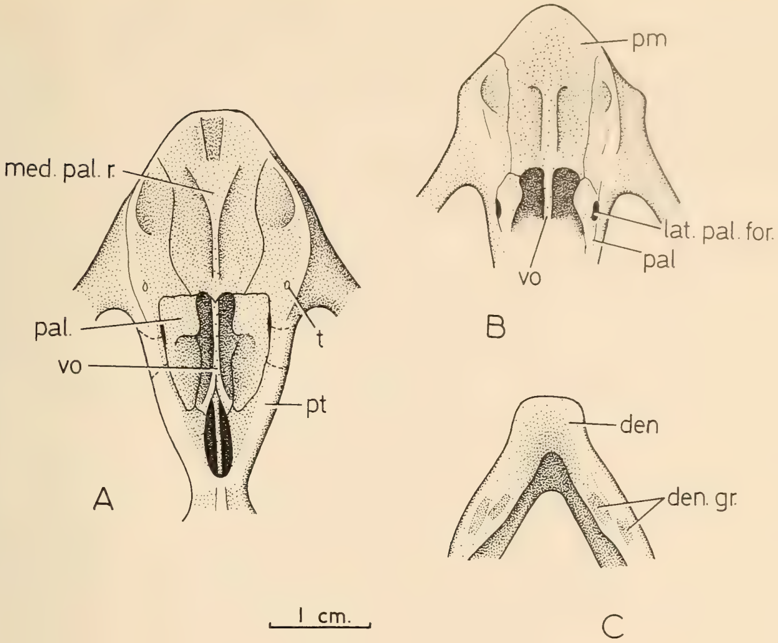

Fig. 5. A. *Emydops longus* paratype B.M.(N.H.) R4957. Palate, $\times \frac{3}{2}$. B–C. *Myosauroides minnaari* type R.C.54, $\times \frac{3}{2}$. Anterior palate and dorsal view of mandible respectively.

COMPARISON WITH OTHER DICYNODONTS

At present, three genera especially appear to have significant resemblances, and possible affinities, with *Myosaurus*. These are *Emydops*, *Cistecephalus* and *Myosauroides*.

The Upper Permian *Emydops* (Fig. 5A) has been mentioned as a possible *Myosaurus* ancestor by Haughton (1917) and, although the genus has many clearly primitive characters, it does include features which deserve consideration. These are a definite palatine-premaxilla contact, a long narrow interpterygoidal vacuity, and a thin, steep vomerine septum dividing the internal nares. The palatine, in contrast to *Myosaurus*, is still well developed and received the bite of the lower jaw teeth during mastication, but in the upper jaw teeth are vestigial and apparently of no great functional significance. In the skull roof the proportions of intertemporal to interorbital width are close to those of *Myosaurus*, but the postorbital is not flared laterally above the temporal fenestra and instead forms the vertical border of the intertemporal bar. A large postfrontal, lost in the more progressive smaller genera, is still present, as is the preparietal. The lower jaw has a row of functional teeth on the medial edge of the dentary, but anteriorly no dentary table is formed and a shovel-like tip, basically similar to that of *Myosaurus*, is formed.

Clearly, *Emydops* itself should not be designated a direct ancestor of *Myosaurus*, but it does none the less possess several characters expected in such an ancestor, and it seems very likely that a more detailed knowledge of *Emydops* and allied forms would reveal a more definite picture of the origins of later groups such as *Myosaurus*.

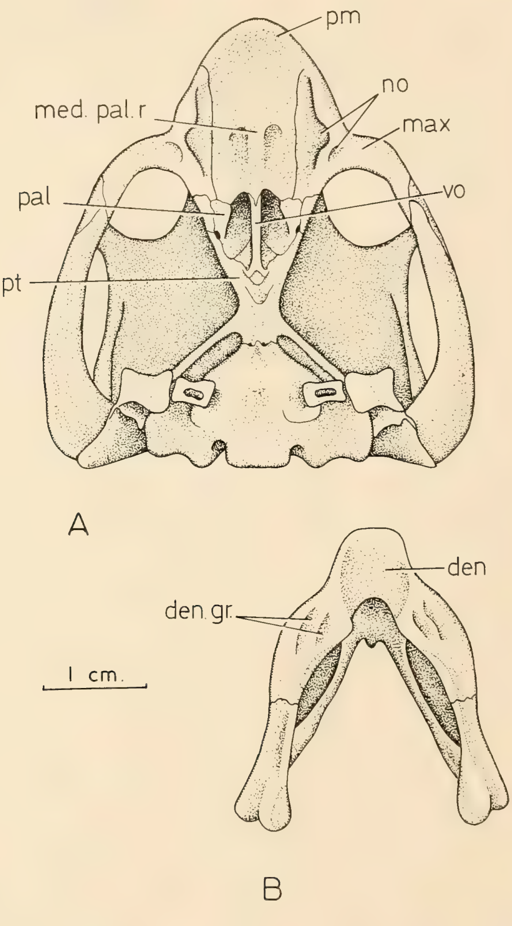

Fig. 6. *Cistecephalus* sp. S.A.M. No. 10665 × $\frac{3}{2}$. A. Ventral view of skull. B. Dorsal view of mandible.

The genus *Cistecephalus* has recently been reviewed by Keyser (1973) and discussed by Cluver (1974), and the skull morphology is now well known (Fig. 6). While there are obvious adaptations to a specialized way of life, several resemblances to *Myosaurus* exist. A postfrontal is absent, as in *Myosaurus*, but the exceptionally wide intertemporal sheet lacks a preparietal. Ventrally the secondary palate has very much the same organization as *Myosaurus*, and anterior palatal ridges are absent and the maxilla is confined to a lateral position. The palatines are small and, as in *Myosaurus*, each is pierced by a foramen. In the lower jaw the dentaries are drawn up anteriorly to a transverse blade, fairly sharp, while laterally a prominent dentary shelf is formed.

Here, however, the similarities cease. In *Cistecephalus* the interpterygoidal vacuity has been obliterated by reinforcement of the basicranial girder, and the vomer is a deep and wide plate with its ventral edge level with the ventral borders of the pterygoids. Anteriorly, two pairs of pockets, one lateral and one medial to the palatal rim, lie at the level of the weak caniniform process; these pit-like depressions seem to be unique to *Cistecephalus*. A wide orbitonasal opening leads into the interior of the snout, while the lacrimal foramen (if present) is unusually placed near the border of this opening. The lower jaw, again, is more powerfully developed in *Cistecephalus* than in *Myosaurus*, and the deep symphyseal region is characteristically scooped out behind the square, shovel-like tip; the dorsal surface of each dentary is widely expanded behind this, and very different to the narrow, weakly developed dentary ramus of *Myosaurus*. When, in addition to these factors, the perforated stapes and secondary widening of the skull roof are taken into consideration, it becomes clear that descent of a form such as *Myosaurus* from this genus is highly improbable, even although certain apparently significant resemblances between the two genera exist.

Myosauroides, the third genus which can be conveniently compared with *Myosaurus*, shows resemblances to both that genus and *Cistecephalus* (Fig. 5B, C). The intertemporal region is of the same width as in *Myosaurus* and also lacks a postfrontal, while a ventral flange of the frontal extends medially in a manner reminiscent of *Myosaurus*. Anterior palatal ridges are lacking, the palatine is weak, and the interpterygoidal vacuity and delicate vomerine septum are almost identical to the *Myosaurus* condition. The jaw symphysis has the same sharply squared-off tip, and the stapes is the usual thin, unperforated rod. *Myosauroides* has a fairly prominent caniniform process and a higher palatal rim than *Myosaurus*, but this rim is continued posteriorly from the caniniform process for a short way as a postcaniniform crest, similar to that of *Myosaurus*. Differences from *Myosaurus*, which are at the same time resemblances to *Cistecephalus*, are the broad, grooved dorsal dentary surfaces, the lack of a preparietal, and the generally still wide orbitonasal passage.

Of the three genera, *Myosauroides* appears to be the closest to *Myosaurus*, and it is quite conceivable that, with the exception of the preparietal, characteristics of *Myosaurus* such as the highly reduced orbitonasal passage and the weak dentary ramus could have been derived from the *Myosauroides* condition. In terms of jaw function, too, *Myosaurus* and *Myosauroides* appear to be broadly similarly adapted, and there is no evidence in *Myosauroides* of lateral jaw displacement during mastication such as is found in *Cistecephalus* (see above). The quadrate-articular surfaces are tightly interlocked and the secondary palate is not significantly wider than the symphyseal region of the lower jaw. However, the lack of a preparietal precludes *Myosauroides minnaari* itself from direct ancestry of *Myosaurus.*

Viewed generally, the three genera *Myosaurus*, *Myosauroides* and *Cistecephalus* appear to be united by fairly clear common characteristics, with *Myosaurus* and *Myosauroides* more closely related to each other than either is to the strongly divergent *Cistecephalus.* If these genera are indeed part of a natural group, this is not reflected in any present classification, where *Cistecephalus* and *Myosaurus*, for instance, are usually placed in separate families (Haughton & Brink 1954; Boonstra 1972; Cluver 1974). In view of the fact, however, that a common origin of the group cannot as yet be convincingly established, and as our knowledge of the many Permian pristerodontinid genera is still very incomplete, it seems unwise to attempt any large-scale classificatory reorganization of the endothiodontids at present.

SUMMARY

The skull of *Myosaurus gracilis* shows several departures from the usual dicynodont condition, especially in the otic capsule, snout, secondary palate and mandible. Perhaps in keeping with its lone survival into the early Triassic, most of these modifications are connected with mastication, and seem to reflect a dietary change. *Myosaurus* shares such features as a broad intertemporal region, lack of a postfrontal, the small palatine and laterally confined maxilla, as well as the absence of anterior palatal ridges and the presence of a square-tipped, shovel-shaped jaw symphysis, with Upper Permian genera such as *Myosauroides* and *Cistecephalus.* While there is a possibility of these three genera belonging to a single natural group, their relationships with the numerous and generally poorly-known Permian endothiodontids remain obscure, and a reorganization of the classification of the Endothiodontidae has not been attempted. Among themselves, *Myosaurus* and *Myosauroides* show the closest relationship, while the more aberrant *Cistecephalus* is strongly specialized in respect of, especially, the skull roof, basicranial axis and palate-mandible relationships.

ACKNOWLEDGEMENTS

I am indebted to Dr J. W. Kitching of the Bernard Price Institute for Palaeontological Research, Johannesburg, for the loan of specimens of *Myosaurus*, and to Mr Richard Rubidge of Wellwood, Graaff-Reinet, for permission to prepare and study the type of *Myosauroides minnaari.* A second specimen of the latter species was lent to me through the kindness of Dr Eugene S. Gaffney of the American Museum of Natural History, New York, while the type and paratype of *Emydops longus* were prepared and studied at the British

Museum (Natural History) through the kind permission of Dr A. J. Charig.

Visits to these two overseas institutions were made possible through study grants from the South African Council for Scientific and Industrial Research, and the Trustees of the South African Museum.

The beautifully prepared type skulls of *Myosaurus gracilis* are testimony to the exceptional skill of Mrs Ione Rudner of the South African Museum.

Mr N. J. Eden was responsible for the photography, and Mr V. Branco prepared the final drawings.

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ABBREVIATIONS

ang.	angular
art.	articular
bas.	basisphenoid
boc.	basioccipital
can. proc.	caniniform process
den.	dentary
den. gr.	dentary gr.
ect.	ectopterygoid
eoc.	exoccipital
ept.	epipterygoid
for.	foramen
for. mag.	foramen magnum
fr.	frontal
gr.	groove
i.c.a.	internal carotid artery opening
ip.	interparietal
ipt. vac.	interpterygoidal vacuity
jug.	jugular
lac.	lacrimal
lat. fl.	lateral flange of squamosal
lat. pal. for.	lateral palatal foramen
max.	maxilla
med. pal. r.	medial palatal ridge on premaxilla
nas.	nasal
no.	notch
nut. ch.	nutrient channel
op.	opisthotic
os.	orbitosphenoid
pa.	parietal
pal.	palatine

pal. for.	palatine foramen
pas.	parasphenoid
pc. cr.	postcaniniform crest
pfr.	prefrontal
pm.	premaxilla
po.	postorbital
pp.	preparietal
prs.	presphenoid
pt.	pterygoid
pt. f.	posttemporal fenestra
q.	quadrate
q. for.	quadrate foramen
q.j.	quadratojugal
sa.	surangular
soc.	supraoccipital
sq.	squamosal
st.	stapes
t.	tooth
tab.	tabular
A.M.N.H.	American Museum of Natural History, New York
B.M.(N.H.)	British Museum (Natural History), London
B.P.I.	Bernard Price Institute for Palaeontological Research, Johannesburg
R.C.	Rubidge Collection, Graaff-Reinet
S.A.M.	South African Museum, Cape Town

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Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a, b*; Liste: 11. Turton, 1932: 80.

Michael A. Cluver

THE CRANIAL MORPHOLOGY OF THE LOWER TRIASSIC DICYNODONT *MYOSAURUS GRACILIS*

507.68

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By

BRIAN KENSLEY

Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R4,00

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1974

ISBN 0 949940 55 0

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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[*MS accepted 15 October 1973*]

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INTRODUCTION

According to the recommendation 72D of the International Code of Zoological Nomenclature (1964), institutions holding type material should publish lists of their type holdings. This is the first of the crustacean type lists of the holdings of the South African Museum, and has been consciously modelled on a publication of the British Museum (Natural History) (Thurston & Allen 1969), as it was felt that the format of the latter was particularly concise and lucid.

The name under which a species was first described is placed in square brackets if this name has since been submerged. The current name is then placed in round brackets, following the original reference.

If a valid species has been transferred from the original to another genus, the current name and reference is followed by the original name in round brackets.

Where one of several specimens of a species from the same locality was sent to T. R. R. Stebbing, who subsequently described it as a new species, the specimens which he did not see are designated as topotypes.

Where a species was described from more than one specimen (even if from a single male and a single female) without a holotype being chosen, the specimens are designated as syntypes.

HISTORICAL DISCUSSION

Much the largest number of undescribed decapods were collected by the S.S. *Pieter Faure*. This was a steam-trawler purchased by the Government of the Cape Colony in 1897, to assist with the first Marine Biological Survey. The survey covered the area from St. Helena Bay in the west to East London and, later, from Cape Vidal in Zululand to the south coast of Natal.

Ann S. Afr. Mus. **66** (4), 1974: 55–80.

The S.S. *Pickle*, a vessel of the Government of the Union of South Africa conducted a marine survey of Moçambique in 1925–6, the results of which were reported on by K. H. Barnard in 1926.

Some undescribed material was obtained by the R/V *Africana II*, largest of the Division of Sea Fisheries research ships.

Material from the south-west Indian Ocean was obtained on the seventh cruise of the United States National Science Foundation R/V *Anton Bruun*, while participating in the International Indian Ocean Expedition in 1964.

The zoology departments of two South African universities have also contributed to the list of new decapod species. These are the University of the Witwatersrand, and the University of Cape Town. The latter has covered much of the coastline of South Africa during surveys of the shore and estuarine fauna, while the operations of the University of Cape Town research ship *John D. Gilchrist* have also yielded undescribed species.

Individual collectors have also contributed to the fauna list. These include J. D. Gilchrist, Government Marine Biologist during the early part of this century, K. H. Barnard, of the South African Museum, and H. W. Bell-Marley of Natal.

CRUSTACEA

DECAPODA

REPTANTIA

BRACHYURA

Family **Majidae**

Subfamily **Inachinae**

ACHAEUS Leach

Achaeus barnardi Griffin, 1968: 81.

Holotype: S.A.M. A1392 (male; chelipeds and pereiopods missing; in alcohol).

Paratypes: S.A.M. A1392 (2 males, 1 ovigerous female; most pereiopods detached; in alcohol).

Locality: Off Cape Morgan, Cape Province, 36 fathoms.

Collected by: S.S. *Pieter Faure*.

Achaeus spinosissimus Griffin, 1968: 76.

Holotype: S.A.M. A8309 (male; most pereiopods detached; in alcohol).

Locality: Off Hood Point, Cape Province, 49 fathoms.

Collected by: S.S. *Pieter Faure*.

PLATYMAIA Miers

Platymaia turbynei Stebbing, 1902: 3.

Syntypes: S.A.M. A1358–A1362 (15 females, 23 males; numerous loose appendages; in alcohol).

Locality: Off Durban, Natal, 440 fathoms.

Collected by: S.S. *Pieter Faure.*

DEHAANIUS Macleay

Dehaanius undulatus Barnard, 1947: 361.

Syntypes: S.A.M. A3131 (2 females; 1 perfect, 1 with all pereiopods detached; dry). S.A.M. A6353 (1 male; carapace broken, 1 cheliped present; dry). S.A.M. A6376 (1 female; all pereiopods detached; dry).

Localities: Durban, Natal; Delagoa Bay, Moçambique.

Collected by: H. W. Bell-Marley, K. H. Barnard.

Subfamily **Acanthonychinae**

MENAETHIOPS Alcock

Menaethiops delagoae Barnard, 1955: 13.

Holotype: S.A.M. A10906 (male; dry).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Menaethiops natalensis Barnard, 1955: 13.

Syntypes: S.A.M. A10904 (male; dry). S.A.M. A10905 (1 male, 2 females; dry).

Localities: S.A.M. A10904 Umpangazi, Natal. S.A.M. A10905 Delagoa Bay, Moçambique.

Collected by: University of Cape Town, University of the Witwatersrand.

Subfamily **Pisinae**

EURYNOME Leach

Eurynome elegans Stebbing, 1921: 454.

Holotype: S.A.M. A1610 (female; most appendages detached; dry).

Locality: Cape Vidal, Natal NNE¼N, 15 km, 80 fathoms.

Collected by: S.S. *Pieter Faure.*

Family **Hymenosomatidae**

RHYNCHOPLAX Stimpson

Rhynchoplax bovis Barnard, 1947: 362.

Syntypes: S.A.M. A8454 (male; pereiopods missing; in alcohol). S.A.M. A8336 (3 females; most appendages detached; in alcohol).

Localities: S.A.M. A8454, 25 km west of East London, Cape Province, 37 fathoms. S.A.M. A8336, Port Elizabeth, Cape Province.

Collected by: S.S. *Pieter Faure*.

Family **Retroplumidae**

RETROPLUMA Gill

Retropluma planiforma Kensley, 1969: 158.

Holotype: S.A.M. A12644 (female; 3 pereiopods missing; in alcohol).

Paratypes: S.A.M. A12643, A12645 (2 males, 3 females; several appendages missing or detached; in alcohol).

Locality: 29.37S, 31.33E, 175–200 metres.

Collected by: R/V *Anton Bruun*, 7th Cruise.

Family **Palicidae**

PALICUS Philippi

Palicus sexlobata Kensley, 1969: 156.

Holotype: S.A.M. A12642 (male; 1 chela, 2 pereiopods detached, rest missing; in alcohol).

Locality: 24.46S, 35.18E, 110 metres.

Collected by: R/V *Anton Bruun*, 7th Cruise.

Family **Ocypodidae**

CLEISTOSTOMA de Haan

Cleistostoma algoense Barnard, 1954: 122.

Syntypes: S.A.M. A850 (1 ovigerous female; carapace, most pereiopods detached; in alcohol). S.A.M. A8493 (1 ovigerous female; 3 males; all pereiopods detached; dry).

Locality: Zwartkops Estuary, near Port Elizabeth, Cape Province.

Collected by: University of Cape Town.

PARACLEISTOSTOMA de Man

Paracleistostoma fossula Barnard, 1955: 24.

Holotype: S.A.M. A10778 (ovigerous female; all pereiopods detached; in alcohol).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Family **Grapsidae**

ILYOGRAPSUS Barnard

[*Ilyograpsus rhizophorae*] Barnard, 1955: 26. (Transferred to *I. paludicola* (Rathbun) by Crosnier, 1965.)

Holotype: S.A.M. A10913 (male; all pereiopods detached; in alcohol).

Locality: Inhambane, Moçambique.

Collected by: University of Cape Town.

Family **Portunidae**

LUPOCYCLUS Adams & White

Lupocyclus tugelae Barnard, 1950: 148.

Holotype: S.A.M. A8320 (female; 4 detached pereiopods; dry).

Locality: Off Tugela River mouth, Natal, 36 fathoms.

Collected by: S.S. *Pieter Faure.*

THALAMITA Latreille

Thalamita delagoae Barnard, 1950: 178.

Holotype: S.A.M. A10870 (male; all pereiopods detached; dry).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

[*Thalamita inhacae*] Barnard, 1950: 179. (Transferred to *T. bouvieri* Nobili, by Crosnier, 1962.)

Holotype: S.A.M. A10871 (female; 3 pereiopods missing, rest detached; dry).

Locality: Inhaca Island, Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

XAIVA Macleay

Xaiva mcleayi (Barnard), 1947: 363 (as *Portumnus mcleayi*).

Syntypes: S.A.M. A631, A632 (3 males, 6 females; in alcohol).

Localities: Algoa Bay, Cape Province, to Port Shepstone, Natal.

Collected by: S.S. *Pieter Faure.*

Family **Xanthidae**

Section *HYPEROMERISTA*

DAIROIDES Stebbing

Dairoides margaritatus Stebbing, 1920: 234.

Syntypes: S.A.M. A1606 (2 males; 1 dry, carapace fragmented, 1 in alcohol).

Locality: Durnford Point, Natal NM¾W, 19 km, 90 fathoms.

Collected by: S.S. *Pieter Faure.*

LYBIA Milne Edwards

Lybia plumosa Barnard, 1947: 364.

Holotype: S.A.M. A10847 (female; all pereiopods detached; dry).

Locality: Umtwalumi, Natal.

Collected by: University of Cape Town.

Family **Goneplacidae**

HEXAPUS de Haan

Hexapus stebbingi Barnard, 1947: 366.

Syntypes: S.A.M. A434–7, A847–8, A1611 (5 ovigerous females, 13 females, 7 males; in alcohol).

Localities: S.A.M. A434–7, Sebastian Bay, Cape Province, 20–34 fathoms. A847, 33.52S, 25.43E, 16½ fathoms. A848, Riet Point, Cape Province, NE by E, 3 km, 23 fathoms. A1611, Cape St. Blaize, Cape Province, SW by W¼W, 10 km, 15 fathoms.

Collected by: S.S. *Pieter Faure.*

OMMATOCARCINUS White

Ommatocarcinus pulcher Barnard, 1950: 286.

Holotype: S.A.M. A8322 (male; 6 pereiopods detached; in alcohol).

Locality: Natal coast, 28 fathoms.

Collected by: H. W. Bell-Marley.

THAUMASTOPLAX Miers

Thaumastoplax spiralis Barnard, 1950: 301.

Syntypes: S.A.M. A8487 (3 males, 1 female; in alcohol).

Locality: Off St. Helena Bay, Cape Province.

Collected by: S.S. *Pieter Faure.*

XENOPHTHALMODES Richters

Xenophthalmodes brachyphallus Barnard, 1955: 34.

Syntypes: S.A.M. A10825 (1 male, 1 female; dry).

Locality: Inhambane, Moçambique.

Collected by: University of Cape Town.

Family **Dromiidae**

CRYPTODROMIOPSIS Borradaile

Cryptodromiopsis bituberculata (Stebbing), 1920: 254 (as *Eudromia bituberculata*).

Holotype: S.A.M. A858 (female; carapace detached; in alcohol).

Locality: Off Rooi Els River, False Bay, Cape Province, 18 fathoms.

Collected by S.S. *Pieter Faure*.

Cryptodromiopsis lepidota Barnard, 1947: 369.

Holotype: S.A.M. A814 (female; 2 pereiopods detached; dry).

Locality: Off Hood Point Lighthouse, near East London, Cape Province, 49 fathoms.

Collected by: S.S. *Pieter Faure*.

DROMIDIA Stimpson

Dromidia aegibotus Barnard, 1947: 366.

Syntypes: S.A.M. A769 (1 male, 1 female; in alcohol). S.A.M. A770 (1 male, 1 female; in alcohol). S.A.M. A778 (1 male; in alcohol).

Localities: S.A.M. A769, False Is., Algoa Bay, Cape Province, 38 fathoms. S.A.M. A770, False Bay, Cape Province. S.A.M. A778, Rocky Bank, False Bay, Cape Province, 17–27 fathoms.

Collected by: S.S. *Pieter Faure*.

Dromidia dissothrix Barnard, 1947: 367.

Holotype: S.A.M. A879 (1 female; 7 pereiopods detached; dry).

Locality: Off Hout Bay, Cape Province.

Collected by S.S. *Pieter Faure*.

DROMIDIOPSIS Borradaile

Dromidiopsis cornuta Barnard, 1947: 367.

Syntypes: S.A.M. A856 (male; all pereiopods detached; dry). S.A.M. A8237 (female; all pereiopods detached; dry).

Localities: S.A.M. A856, Cape St. Blaize, Cape Province, NE$\frac{3}{4}$N, 16 km, 39 fathoms. S.A.M. A8237, False Bay, Cape Province, 23 fathoms.

Collected by: S.S. *Pieter Faure*.

EUDROMIDIA Barnard

Eudromidia hendersoni (Stebbing), 1921: 462 (as *Eudromia hendersoni*).

Holotype: S.A.M. A813 (female; carapace and pereiopods detached; dry).

Locality: False Bay, Cape Province, 19 fathoms.

Collected by: S.S. *Pieter Faure*.

PETALOMERA Stimpson

Petalomera laevis Kensley, 1970: 111.

Holotype: S.A.M. A12824 (Ovigerous female; in alcohol).

Paratype: S.A.M. A12825 (male; in alcohol).

Locality: Jangamo, Moçambique.

Collected by: University of Cape Town.

Family **Dynomenidae**

[***MAXILLOTHRIX***] Stebbing

[*Maxillothrix actaeiformis*] Stebbing, 1921: 457. (Transferred to *Dynomene pilumnoides* Alcock, by Barnard, 1947.)

Syntypes: S.A.M. A839 (1 male, 3 females; most appendages detached; in alcohol).

Locality: Umhlangakulu River, Natal, NW by N, 12 km, 50 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Homolidae**

HOMOLA Leach

Subgenus ***PAROMOLA*** Wood-Mason

Homola (*Paromola*) *alcocki* (Stebbing), 1920: 255 (as *Latreillopsis alcocki*).

Holotype: S.A.M. A1450 (female; carapace detached; in alcohol).

Locality: Algoa Bay, Cape Province, 40 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Leucosiidae**

EBALIA Leach

Ebalia agglomus Barnard, 1955: 39.

Holotype: S.A.M. A10739 (male; carapace fragmented; pereiopods excluding chelipeds missing; dry).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Ebalia (*Lithadia*) *barnardi* Stebbing, 1920: 248.

Holotype: S.A.M. A504 (female; all pereiopods detached; dry).

Locality: Umhloti River, Natal, NW by W¾W, 4 km, 25 fathoms.

Collected by: S.S. *Pieter Faure*.

Ebalia glomus Stebbing, 1921: 460.

Syntypes: S.A.M. A503 (1 male, 1 female; all pereiopods detached; dry).

Locality: Umhloti River, Natal, NNW, 2 km, 27 fathoms.

Collected by: S.S. *Pieter Faure*.

[*Nursia postulans*] Stebbing, 1921: 461. (Transferred to *Ebalia tuberculosa* (M. Edw.) by Barnard, 1950.)

Holotype: S.A.M. A502 (1 male; carapace and pereiopods detached; dry).

Locality: Cape Natal, W by N¾N, 17 km, 185 fathoms.

Collected by: S.S. *Pieter Faure*.

HETERONUCIA Alcock

Heteronucia angulata Barnard, 1947: 372.

Holotype: S.A.M. A8210 (1 female; all pereiopods detached; dry).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Family **Tymolidae**

CORYCODUS Milne Edwards

Corycodus disjunctipes (Stebbing), 1910: 340 (as *Nasinatalis disjunctipes*).

Syntypes: S.A.M. A516, A517, (3 females; dry, in same container as S.A.M. A1456 & A1609).

Locality: Cape Natal, NW½W, 9 km, 62 fathoms.

Collected by: S.S. *Pieter Faure*.

CYMONOMUS Milne Edwards

Cymonomus trifurcus Stebbing, 1920: 245.

Holotype: S.A.M. A884 (1 male; carapace and all appendages detached; dry).

Locality: Buffalo River, Cape Province, NW½W, 30 km, 300 fathoms.

Collected by: S.S. *Pieter Faure*.

ETHUSA Roux

Ethusa sinespina Kensley, 1969: 161.

Holotype: S.A.M. A12648 (1 ovigerous female; pereiopods detached; in alcohol).

Paratype: S.A.M. A12649 (1 female; 7 pereiopods missing; in alcohol).

Localities: A12648, 29.42S, 31.38E, 350 metres. A12649, 29.35S, 31.42E, 138 metres.

Collected by: R/V *Anton Bruun*, 7th Cruise.

XEINOSTOMA Stebbing

Xeinostoma eucheir Stebbing, 1920: 243.

Syntypes: S.A.M. A1608 (1 male, 1 female; several pereiopods detached; dry).

Locality: Cape Vidal, Natal, NNE$\frac{1}{4}$N, 15 km, 90 fathoms.

Collected by: S.S. *Pieter Faure.*

ANOMURA

Family **Lithodidae**

NEOLITHODES Milne Edwards & Bouvier

Neolithodes asperrimus Barnard, 1947: 374.

Syntypes: S.A.M. A6371 (1 male; dry, 1 female; in alcohol).

Locality: Off Saldanha Bay, Cape Province, 300 fathoms.

Collected by: Trawler *Ben Holden*, Cape Town.

Neolithodes capensis Stebbing, 1905: 70.

Topotype: S.A.M. A8230 (1 ovigerous female; in alcohol).

Locality: Off Cape Point Cape Province, N 70° E, 64 km, 800 fathoms.

Collected by: ?

Family **Pomatochelidae**

POMATOCHELES Miers

Pomatocheles balssi Stebbing, 1914: 3.

Holotype: S.A.M. A1571 (1 male; carapace and appendages detached; dry).

Locality: Cove Rock, Cape Province, NW$\frac{3}{4}$W, 21 km, 80–130 fathoms.

Collected by: S.S. *Pieter Faure.*

Family **Paguridae**

ANAPAGURUS Henderson

Anapagurus hendersoni Barnard, 1947: 377.

Syntypes: S.A.M. A1500–03, (7 males, 1 female, 5 ovigerous females; in alcohol). S.A.M. A8225–6 (1 male; in alcohol).

Localities: S.A.M. A1500, Bird Island passage, Cape Province, 10 fathoms. A1501, Cape Natal, W by N, 10 km, 48 fathoms. A1502, Umhloti River, Natal, NW$\frac{1}{2}$W, 24 km, 100 fathoms. A1503, Cape Natal, W by N, 10 km, 54 fathoms. A8225, East London, Cape Province, NW$\frac{1}{2}$N, 32 km, 400 fathoms.

Collected by: S.S. *Pieter Faure.*

CANCELLUS Milne Edwards

Cancellus makrothrix Stebbing, 1924: 6.

Topotype: S.A.M. A1541 (1 male; in alcohol).

Locality: Bird Island passage, Cape Province, 10 fathoms.

Collected by: S.S. *Pieter Faure*.

DIOGENES Dana

Diogenes extricatus Stebbing, 1910: 355.

Holotype: S.A.M. A1491 (male; in alcohol).

Locality: Off Seal Island, Mossel Bay, Cape Province.

Collected by: S.S. *Pieter Faure*.

PAGURISTES Dana

Paguristes barnardi Forest, 1954: 208.

Syntypes: S.A.M. A12779 (3 males; in alcohol). S.A.M. A12780 (2 males, 1 ovigerous female; in alcohol).

Localities: S.A.M. A12779, Agulhas, Cape Province. S.A.M. A12780, Arniston, Cape Province.

Collected by: University of Cape Town.

Paguristes engyops Barnard, 1947: 375.

Syntypes: S.A.M. A3255 (3 males, 1 female, 3 ovigerous females; in alcohol).

Locality: Buffels Bay, Cape Province.

Collected by: K. H. Barnard.

Paguristes macrotrichus Forest, 1954: 211.

Holotype: S.A.M. A851 (female; in alcohol).

Locality: Umhlangakulu River, Natal, NW by N, 12 km, 50 fathoms.

Collected by: S.S. *Pieter Faure*.

[*Paguristes rosaceus*] Barnard, 1947: 375. (Transferred to *Paguristes gamianus* H. Milne Edwards by Forest, 1954.)

Syntypes: S.A.M. A8452 (3 ovigerous females; in alcohol).

Locality: Off Keurbooms River, Cape Province.

Collected by: K. H. Barnard.

PARAPAGURUS Smith

[*Parapagurus bouvieri*] Stebbing, 1910: 357. (Transferred to *Parapagurus pilosimanus* Smith, see Barnard, 1950.)

Syntype: S.A.M. A1524 (female; in alcohol).

Locality: Buffalo River, Cape Province, NW½W, 30 km, 300 fathoms.

Collected by: S.S. *Pieter Faure*.

Parapagurus kilburni Kensley, 1973: 285.

Holotype: S.A.M. A13185 (male; in alcohol).

Paratypes: S.A.M. A13186 (4 males; in alcohol).

Locality: Off Durban, 270 metres.

Collected by: R. N. Kilburn, Natal Museum.

PYLOPAGURUS Milne Edwards & Bouvier

Pylopagurus liochele Barnard, 1947: 376.

Syntypes: S.A.M. A1543 (female; abdomen missing; in alcohol). S.A.M. A4038 (male; abdomen and pereiopods detached; in alcohol).

Localities: A1543, Bird Island passage, Cape Province, 10 fathoms. A4038, Cape Seal, Cape Province W¾S, 9 km, 37 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Porcellanidae**

PISIDIA Leach

Pisidia delagoae (Barnard), 1955: 40 (as *Porcellana delagoae*, see Haig, 1965).

Holotype: S.A.M. A10703 (1 ovigerous female; pereiopods detached; in alcohol).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Family **Uroptychidae**

HAPALOPTYX Stebbing

Hapaloptyx difficilis Stebbing, 1920: 263.

Holotype: S.A.M. A1440 (1 ovigerous female; carapace and appendages detached; dry; 3 slides).

Locality: Scottburgh light house, Natal, NW by W, 13 km, 92 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Galatheidae**

MUNIDOPSIS Whiteaves

Munidopsis barnardi Kensley, 1968: 290.

Holotype: S.A.M. A12636 (female; in alcohol).

Paratypes: S.A.M. A10497, A10508 (4 males; in alcohol). S.A.M. A10465. (2 males; in alcohol). S.A.M. A10485 (1 male, 1 female; in alcohol).

Locality: Off Cape Point, Cape Province, 2 708–3 038 metres.
Collected by: R/V *Africana II.*

Munidopsis chacei Kensley, 1968: 288.
Holotype: S.A.M. A10470 (ovigerous female; in alcohol).
Locality: Off Cape Point, Cape Province, 2 745 metres.
Collected by: R/V *Africana II.*

Family **Axiidae**

METICONAXIUS de Man

Meticonaxius longispina (Stebbing), 1920: 265 (as *Axius longispina*).
Holotype: S.A.M. A957 (1 slide plus fragments in alcohol).
Locality: Cape Morgan, Cape Province, NNW, 11 km, 52 fathoms.
Collected by: S.S. *Pieter Faure.*

CALOCARIS Bell

Calocaris (*Calocaris*) *barnardi* Stebbing, 1914: 9.
Syntypes: S.A.M. A1549 (2 females; dry, 1 female; in alcohol).
Locality: Cape Castle, E½N, 21 km, 120 fathoms.
Collected by: S.S. *Pieter Faure.*

Family **Callianassidae**

CALLIANASSA Leach

Callianassa adamas Kensley, 1974: 266.
Holotype: S.A.M. A12103 (male; in alcohol).
Allotype: S.A.M. A12103 (female; in alcohol).
Paratype: S.A.M. A10985 (male; in alcohol).
Localities: S.A.M. A12103, Orange River mouth, 10–35 metres. S.A.M. A10985, Olifants River mouth.
Collected by: Diamond dredge *Emerson—K.*

Callianassa gilchristi Barnard, 1947: 379.
Syntypes: S.A.M. A942 (female; in alcohol). S.A.M. A6807 (2 males; several pereiopods detached; in alcohol).
Locality: False Bay, Cape Province.
Collected by: S.S. *Pieter Faure.*

Callianassa kraussi Stebbing, 1900: 39.
Syntypes: S.A.M. A941 (4 specimens; dry, in same bottle as several from other localities).

Locality: Gordon's Bay, Cape Province.

Collected by: S.S. *Pieter Faure*.

Callianassa natalensis Barnard, 1947: 379.

Holotype: S.A.M. A8339 (female; 7 pereiopods detached; in alcohol).

Locality: Natal coast, from stomach of rock cod.

Collected by: H. W. Bell-Marley.

Callianassa subterranea australis Kensley, 1974: 271.

Holotype: S.A.M. A13531 (male; in alcohol).

Allotype: S.A.M. A13532 (female; in alcohol).

Paratypes: S.A.M. A13533–4 (1 male, 1 female; in alcohol). S.A.M. A12103 (1 female; in alcohol).

Localities: S.A.M. A13531—4, Lüderitzbucht, South West Africa. S.A.M. A12103, Orange River mouth.

Collected by: University of Cape Town. Diamond dredge *Emerson—K.*

Family **Upogebiidae**

UPOGEBIA Leach

Upogebia assisi Barnard, 1947: 381.

Holotype: S.A.M. A4348 (1 female; pereiopods detached; in alcohol).

Locality: St. Francis Bay, Cape Province.

Collected by: S.S. *Pieter Faure*.

PALINURA

Family **Palinuridae**

PROJASUS George & Grindley

Projasus parkeri (Stebbing), 1902: 38 (as *Jasus parkeri*).

Holotype: S.A.M. A993 (male; in alcohol).

Topotypes: S.A.M. A994–6. (2 females, 2 ovigerous females, 3 males).

Locality: Buffalo River, Cape Province, N, 24 km, 310 fathoms.

Collected by: S.S. *Pieter Faure*.

PALINURUS Fabricius

Palinurus gilchristi Stebbing, 1900: 31.

Syntype: S.A.M. A970 (male; 8 periopods missing; in alcohol).

Topotype: S.A.M. A971 (male; 1 pereiopod missing; in alcohol).

Locality: False Bay, Cape Province.

Collected by: S.S. *Pieter Faure*.

Palinurus delagoae Barnard, 1926. (See Berry & Plante 1973.)
Neotype: S.A.M. A13179 (male; in alcohol).
Locality: Off Tongaat, Natal.
Collected by: P. Berry, Oceanographic Research Institute, Durban.

PALINUSTUS Milne Edwards

Palinustus mossambicus Barnard, 1926: 126.
Holotype: S.A.M. A10684 (male; 5 pereiopods missing; in alcohol).
Locality: Moçambique, 25.0S, 33.10E, 406 metres.
Collected by: S.S. *Pickle.*

Family **Eryonidae**

POLYCHELES Heller

Polycheles demani Stebbing, 1917: 28.
Paratype: S.A.M. A4343 (male; in alcohol).
Topotypes: S.A.M. A1004–10, off Cape Point, (2 males, 6 females; in alcohol).
Locality: Cape Point, Cape Province, NE by E½E 67 km, 1 645 metres.
Collected by: S.S. *Pieter Faure.*

WILLEMOESIA Grote

Willemoesia bonaspei Kensley, 1968: 294.
Holotype: S.A.M. A10543 (ovigerous female; chelipeds missing; in alcohol).
Paratypes: S.A.M. A10473 (2 males; in alcohol). S.A.M. A10509 (1 female, 2 males; in alcohol). S.A.M. A12637 (2 males; in alcohol).
Locality: Off Cape Point, Cape Province, 2 708–3 038 metres.
Collected by: R/V *Africana II.*

NATANTIA

PENAEIDEA

Family **Penaeidae**

Subfamily **Penaeinae**

PENAEUS Fabricius

[*Penaeus caeruleus*] Stebbing, 1905: 77. (Transferred to *Penaeus monodon* Fabricius, see Barnard, 1950.)
Syntypes: S.A.M. 1039 (3 specimens in bottle with A1040, A1041; in alcohol).
Locality: Nahoon River, East London, Cape Province.
Collected by: S.S. *Pieter Faure.*

PENAEOPSIS Bate

[*Penaeopsis spinulicauda*] Stebbing, 1914: 17. (Transferred to *Metapenaeus monoceros* (Fabricius), see Barnard 1950.)

Syntypes: S.A.M. A2231 (2 specimens, in same bottle as A1203; in alcohol).

Locality: Durban Bay, Natal.

Collected by: K. H. Barnard.

Subfamily **Solenocerinae**

SOLENOCERA Lucas

Solenocera africanum Stebbing, 1917: 32.

Syntypes: S.A.M. A1213 (1 female, few appendages of male; in alcohol).

Locality: Sebastian Bluff (Agulhas Bank), Cape Province, NW¾W, 13 km, 34 fathoms.

Collected by: S.S. *Pieter Faure*.

Solenocera algoense Barnard, 1947: 383.

Holotype: S.A.M. A1211 (male; in alcohol).

Locality: Nanquas Peak, Cape Province, N, 12 km, 50 fathoms.

Collected by: S.S. *Pieter Faure*.

Solenocera comatum Stebbing, 1915: 67.

Syntypes: S.A.M. A1217 (1 male; in alcohol). S.A.M. A1218 (1 female; in alcohol).

Locality: Off East London, Cape Province, 43–50 fathoms.

Collected by: S.S. *Pieter Faure*.

HYMENOPENAEUS Smith

Hymenopenaeus (*Haliporoides*) *triarthrus* (Stebbing), 1914: 21 (as *Haliporoides triarthrus*).

Syntypes: S.A.M. A3940 (3 specimens in bottle with several others; in alcohol).

Locality: East London, Cape Province, NW½N, 29 km, 250–300 fathoms.

Collected by: S.S. *Pieter Faure*.

Subfamily **Aristaeinae**

PLESIOPENAEUS Bate

Plesiopenaeus nitidus Barnard, 1947: 383.

Syntypes: S.A.M. A1193, A1260 (3 females, 3 males; in alcohol).

Locality: Off Cape Point, Cape Province, 500–630 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Sergestidae**

SERGESTES Milne Edwards

[*Sergestes gloriosus*] Stebbing, 1905: 84. (Transferred to *Sergestes prehensilis* Bate by Yaldwyn 1957.)

Syntypes: S.A.M. A1050 (4 specimens, along with several specimens from the same and other localities; in alcohol).

Locality: Sandy Point, Cape Province, NW by W, 27 km, 300 fathoms.

Collected by: S.S. *Pieter Faure*.

ACETES Milne Edwards

Acetes natalensis Barnard, 1955: 43.

Syntypes: S.A.M. A11976 (2 males, 3 females; in alcohol, 1 slide of male petasma).

Locality: Durban Bay, Natal.

Collected by: University of Cape Town.

CARIDEA

Family **Stylodactylidae**

STYLODACTYLUS Milne Edwards

Stylodactylus stebbingi Hayashi & Miyake, 1968: 595.

Holotype: S.A.M. A1285 (male; in alcohol).

Paratypes: S.A.M. A1284–6 (11 ovigerous females, 1 female, 2 males; in alcohol).

Localities: S.A.M. A1284–5, Buffalo River, Cape Province, NW½W, 30 km, 300 fathoms. S.A.M. A1286 South Head, Cape Province, E by S½S, 24 km, 190 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Oplophoridae**

NOTOSTOMUS Milne Edwards

Notostomus auriculatus Kemp, *ined.* (see Barnard 1950).

Holotype: S.A.M. A1189 (female; in alcohol).

Locality: Off Cape Point, Cape Province, 800 fathoms.

Collected by: S.S. *Pieter Faure*.

Family **Hippolytidae**

EUALUS Thallwitz

Eualus ctenifera (Barnard), 1950: 696 (as *Spirontocaris ctenifera*).

Syntypes: S.A.M. A6809 (1 ovigerous female; in alcohol). S.A.M. A8402

(2 ovigerous females, 2 females, 2 males; in alcohol). S.A.M. A8413 (1 ovigerous female; in alcohol).

Localities: S.A.M. A6809, northern Natal coast, 70 fathoms. S.A.M. A8402, 33.49S, 25.56E S.A.M. A8413, Durban, Natal.

Collected by: H. W. Bell-Marley, and S.S. *Pieter Faure*.

Eualus pax (Stebbing), 1915: 91 (as *Spirontocaris pax*).

Allotype: S.A.M. A3944 (ovigerous female; in alcohol).

Locality: Buffels Bay, Cape Province, 30 fathoms.

Collected by: S.S. *Pieter Faure*.

HIPPOLYTE Leach

Hippolyte palliola Kensley, 1970: 183

Holotype: S.A.M. A12710 (male; in alcohol).

Allotype: S.A.M. A12711 (ovigerous female; in alcohol).

Paratypes: S.A.M. A12712 (11 males; in alcohol).

Locality: 8 km south of Kunene River mouth, S.W.A.

Collected by: South African Museum and State Museum, Windhoek.

HIPPOLYSMATA Stimpson

Hippolysmata (*Exhippolysmata*) *tugelae* Stebbing, 1915: 94.

Syntype: S.A.M. A1274 (1 specimen, in same container as topotypes; in alcohol).

Topotypes: S.A.M. A1274 (21 specimens; in alcohol).

Locality: Off south head of Tugela River, Natal, 12 fathoms.

Collected by: S.S. *Pieter Faure*.

LEBBEUS White

Lebbeus saldanhae (Barnard), 1947: 385 (as *Spirontocaris saldanha*).

Holotype: S.A.M. A8446 (female; in alcohol).

Locality: Off Constable Hill, Cape Province, 32 km, 145 fathoms.

Collected by: S.S. *Pieter Faure*.

LEONTOCARIS Stebbing

Leontocaris paulsoni Stebbing, 1905: 99.

Syntypes: S.A.M. A1166 (2 specimens in same container as S.A.M. A1167–72; in alcohol).

Locality: Off Lions Head, Cape Province, 37 km.

Collected by: S.S. *Pieter Faure*.

Family **Processidae**

PROCESSA Leach

Processa austroafricana Barnard, 1947: 386.

Syntypes: S.A.M. A1097–1104 (many specimens in alcohol).

Localities: A1097, Cape St. Blaize, Cape Province, 40 fathoms. A1098, Algoa Bay, Cape Province, 10–16 fathoms. A1099, off Knysna Heads, Cape Province. A1100, Cape St. Blaize, Cape Province, 40 fathoms. A1101, off Struys Point, Cape Province, 42 fathoms. A1102, False Island, Cape Province, 49 fathoms. A1103, off Great Fish Point lighthouse, Cape Province, 40 fathoms. A1104, off Bird Island lighthouse, Cape Province, 57 fathoms.

Collected by: S.S. *Pieter Faure.*

Family **Glyphocrangonidae**

GLYPHOCRANGON Milne Edwards

Glyphocrangon dentatus Barnard, 1947: 387.

Topotype: S.A.M. A8403 (male; dry).

Locality: Moçambique.

Collected by: S.S. *Pickle.*

Family **Ogyrididae**

OGYRIDES Stebbing

Ogyrides saldanhae Barnard, 1947: 387.

Syntypes: S.A.M. A1298 (70 specimens; in alcohol).

Locality: Saldanha Bay, Cape Province, 10 fathoms.

Collected by: S.S. *Pieter Faure.*

Family **Alpheidae**

ALPHEUS Fabricius

Alpheus bullatus Barnard, 1955: 45.

Syntype: S.A.M. A10624 (male; large chela detached; in alcohol).

Locality: Delagoa Bay, Moçambique.

Collected by: University of the Witwatersrand.

Alpheus dissodontonotus Stebbing, 1915: 83.

Holotype: S.A.M. A1561 (ovigerous female; carapace and pereiopods detached; in alcohol).

Locality: 33.50S, 25.46E, 20 fathoms.

Collected by: S.S. *Pieter Faure.*

Alpheus luciae Barnard, 1947: 389.
Holotype: S.A.M. A8423 (1 male; chelipeds detached; in alcohol).
Locality: St. Lucia Bay, Natal.
Collected by: H. W. Bell-Marley.

Alpheus nonalter Kensley, 1969: 172.
Holotype: S.A.M. A12650 (ovigerous female; in alcohol).
Allotype: S.A.M. A12651 (male; in alcohol).
Locality: 29.37S, 31.33E, 175–200 metres.
Collected by: R/V *Anton Bruun*, 7th Cruise.

Alpheus waltervadi Kensley, 1969: 175.
Holotype: S.A.M. A12646 (ovigerous female; in alcohol).
Paratype: S.A.M. A12647 (ovigerous female; in alcohol).
Locality: Walter's Shoal, 33.13S, 43.51E, 38–46 metres.
Collected by: R/V *Anton Bruun*, 7th Cruise.

BETAEUS Dana

Betaeus jucundus Barnard, 1947: 388.
Holotype: S.A.M. A7807 (ovigerous female; in alcohol).
Locality: Keurbooms River, Cape Province.
Collected by: K. H. Barnard.

SALMONEUS Holthuis

Salmoneus rostratus Barnard, 1962: 240.
Syntypes: S.A.M. A11086 (2 ovigerous females; in alcohol).
Locality: Nosy Bé, Madagascar.
Collected by: University of the Witwatersrand.

SYNALPHEUS Bate

Synalpheus anisocheir Stebbing, 1915: 86.
Holotype: S.A.M. A1555 (ovigerous female; few appendages; in alcohol).
Locality: Gordon's Bay, Cape Province.
Collected by: J. D. Gilchrist.

Family **Palaemonidae**

Subfamily **Palaemoninae**

LEANDER Desmarest

[*Leander gilchristi*] Stebbing, 1915: 75. (Transferred to *Palaemon pacificus* (Stimpson) by Barnard 1950, 1955.)
Holotype: S.A.M. A3943 (ovigerous female; in alcohol).

Locality: East London, Cape Province.
Collected by J. D. Gilchrist.

[*Leander peringueyi*] Stebbing, 1915: 75. (Transferred to *Palaemon pacificus* (Stimpson) by Barnard 1950, 1955).
Holotype: S.A.M. A1276 (ovigerous female; in alcohol).
Locality: 33.49S, 25.56E.
Collected by: S.S. *Pieter Faure*.

PALAEMON Fabricius

[*Palaemon delagoae*] Stebbing, 1915: 74. (Transferred to *Macrobrachium equidens* (Dana) by Holthuis 1950.)
Holotype: S.A.M. A2196 (male; chelipeds detached; in alcohol).
Locality: Delagoa Bay, Moçambique.
Collected by: A. W. Bayly.

Subfamily **Pontoniinae**

ISCHNOPONTONIA Bruce

Ischnopontonia lophos (Barnard), 1962: 242 (as *Philarius lophos*).
Holotype: S.A.M. A10652 (ovigerous female; chelipeds detached; in alcohol).
Allotype: S.A.M. A12296 (male; carapace and chelipeds detached; in alcohol).
Locality: Inhaca Island, Delagoa Bay, Moçambique.
Collected by: University of the Witwatersrand.

PERICLIMENAEUS Borradaile

Periclimenaeus uropodialis Barnard, 1958: 18.
Holotype: S.A.M. A10650 (females; carapace and several pereiopods detached; in alcohol).
Locality: Delagoa Bay, Moçambique.
Collected by: University of the Witwatersrand.

PERICLIMENES Costa

Periclimenes (*Periclimenes*) *delagoae* Barnard, 1958: 14.
Holotype: S.A.M. A10648 (ovigerous female; carapace and most appendages detached; in alcohol).
Locality: Delagoa Bay, Moçambique.
Collected by: University of the Witwatersrand.

Family **Crangonidae**

METACRANGON Zarenkov

Metacrangon jacqueti bellmarleyi (Stebbing, 1914: 29) (as *Sclerocrangon bellmarleyi*).

Syntypes: S.A.M. A1077 (male; in alcohol). S.A.M. A1564 (female; in alcohol).

Locality: Cape Natal, N by E, 38 km, 440 fathoms.

Collected by: S.S. *Pieter Faure*.

PONTOPHILUS Leach

Pontophilus megalocheir (Stebbing), 1915: 71 (as *Philocheras megalocheir*).

Holotype: S.A.M. A1317 (female; carapace and most appendages detached; in alcohol).

Locality: Off Cove Rock, East London, Cape Province, 25 fathoms.

Collected by: S.S. *Pieter Faure*.

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By

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Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R4,30

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1974

ISBN 0 949940 56 9

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

THE CRETACEOUS STRATIGRAPHY OF SOUTH-CENTRAL AFRICA

By

MICHAEL R. COOPER

South African Museum, Cape Town

(With 10 figures)

[*Ms. accepted 15 October 1973*]

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INTRODUCTION

Recent studies by Reyment (1969, 1971) have led him to suggest that 'Cretaceous (Albian to Turonian) transgressions around the coast of Africa display a correlative pattern that suggests they may be the results of a see-saw motion' (1971: 1063). Field-work and biostratigraphical studies in Angola, the south-east Cape, Zululand and southern Moçambique do not support this conclusion. A study of the Cretaceous deposits of southern and central Africa suggests the observed sequence of transgressions and regressions can best be explained by eustatic sea-level changes, together with local coastal warping, rather than oscillatory tiltings of the African continent.

STRATIGRAPHY OF THE WEST COAST

Along the west coast of Africa south of the Sahara, i.e. south of latitude 20°N, deposits of Cretaceous age are known from many localities. The occurrence of these sequences is important in the study of the break-up of Gondwanaland and the early history of the South Atlantic Ocean.

According to Furon (1963: 232), the first genuine marine horizon in Ghana is 'that of the Anwiafutu Limestone with *Plicatula auressensis* and *Exogyra olisiponensis*', considered to be of Upper Cenomanian–Turonian age, whilst the earliest marine beds in the Ivory Coast and Upper Volta are assigned to the Upper Cenomanian on the basis of *Plicatula fourneli* Coquand.

The Cretaceous biostratigraphy of Nigeria (Fig. 1) is well known following the studies of Reyment (1954*a*, 1954*b*, 1955, 1965) and Barber (1957). The earliest

Ann. S. Afr. Mus. **66** (5), 1974: 81–107, 10 figs.

recorded marine beds contain *Oxytropidoceras* of low Middle Albian age, this genus dating the maximum transgression of the Albian in Nigeria (Reyment 1955). The remainder of the Albian appears to be present and is in places highly fossiliferous. Undoubted Cenomanian is known only from Calabar Province (Reyment & Tait 1972), where deposits with *Euhystricoceras*, *Turrilites*, *Forbesiceras*, *Acompsoceras* and *Acanthoceras quadratum* Crick occur on the coast. *Euhystricoceras* is confined to Lower Cenomanian strata while the remaining forms are typical of the Middle Cenomanian. The only Upper Cenomanian species so far recorded (Reyment & Tait 1972) is *Metoicoceras* aff. *ornatum* Moreman (= *M. whitei* Hyatt), which indicates an uppermost Cenomanian age (Kennedy 1971).

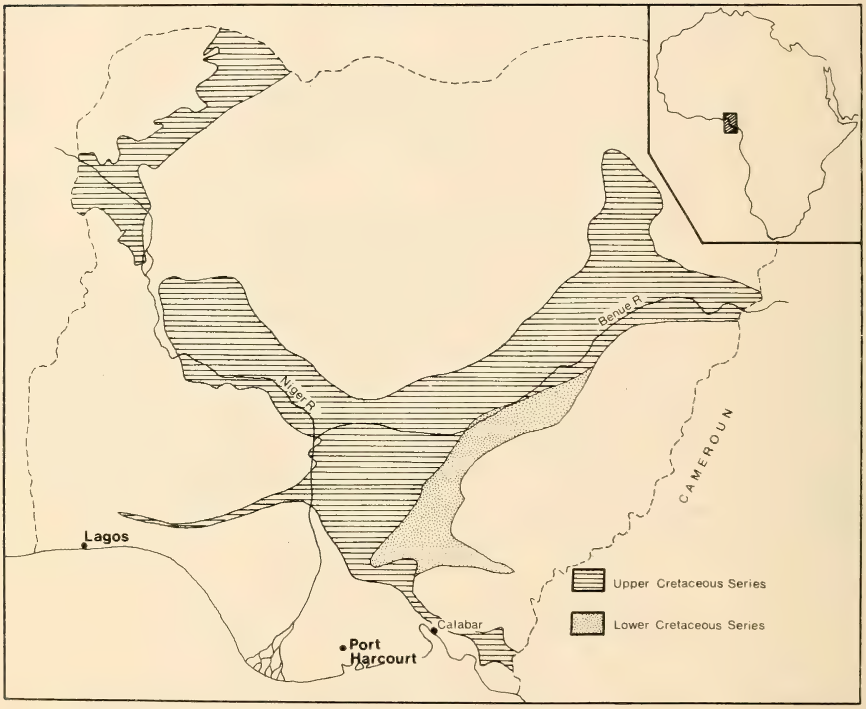

Fig. 1. The Cretaceous outcrop in Nigeria. After Reyment 1955.

The Lower Turonian of Nigeria is very rich in ammonites (Reyment 1954*a*, 1954*b*, 1955; Barber 1957), although Upper Turonian strata appear to be lacking in diagnostic fossils. The Coniacian is well established by the presence of the ammonites *Solgerites*, *Forresteria*, *Peroniceras* (*Peroniceras*), *P.* (*Reginaites*), *Tissotia*, and *Gauthiericeras*. Santonian (?Lower) is known from Nigeria

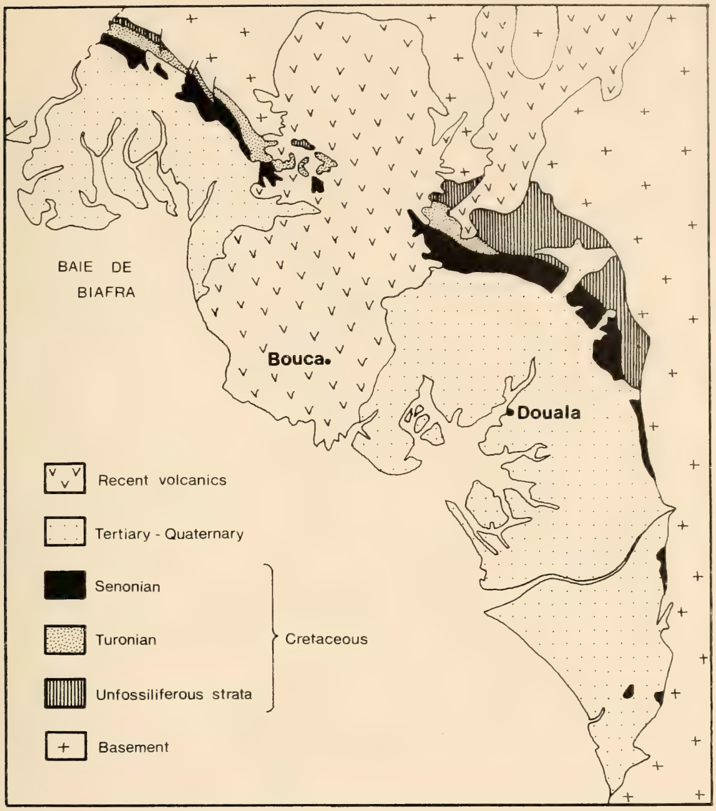

Fig. 2. The distribution of Cretaceous strata in Cameroun. After Belmonte 1966.

and Zaïre by *Texanites.* According to Reyment (1966: 171) ‘The Santonian was, in the Nigerian basin, a time of regression’. This possibly explains the absence of the rich *Pseudoschloenbachia*-fauna which characterizes the Upper Santonian (Collignon 1968) of the east coast. The Campanian and Maastrichtian of Nigeria have yielded *Libycoceras*, *Sphenodiscus*, *Didymoceras* and *Baculites.*

Belmonte (1966) has summarized the latest stratigraphical data concerning the Cretaceous deposits of Cameroun (Fig. 2). Albian is known only from near the Nigerian frontier where cross-bedded sandstones and intercalated shales have yielded plant fragments. Marine Cenomanian has not yet been recorded.

In the Mungo Valley the Cretaceous ‘forment une alternance d'épisodes marins transgressifs’ (Belmonte 1966: 11), and Diebold (1962) has recognized three sedimentary cycles.

The first cycle is a transgressive sequence dated at upper Lower Turonian by the ammonites *Kamerunoceras*, *Neoptychites*, *Choffaticeras*, *Hoplitoides*, etc. The second cycle is a regressive phase dated at Upper Turonian by *Romaniceras* aff. *uchauxiense* (Collignon) and *R.* aff. *deverioides* (de Grossouvre). A transgressive sequence with *Tissotia*, *Barroisiceras*, and *Peroniceras*, dated at Coniacian, constitutes the third cycle.

The Santonian is well developed in the Douala basin, where a marine intercalation has yielded *Texanites quattuornodosus* (Lasswitz) and *T.* aff. *soutoni* (Baily). Reyment (*in* Müller 1966: 140) has recorded the Upper Santonian *Pseudoschloenbachia* from the Mungo River Formation.

In the Douala basin the Campanian is represented by a transgressive sequence yielding the ammonites *Eupachydiscus*, *Karapadites*, *Menabites*, and *Parapuzosia*. These forms suggest a Middle to Upper Campanian age. The presence of *Parapachydiscus stallauense* Imkeller is taken to provide evidence of the Maastrichtian, since this species is known from the Lower Maastrichtian of Nigeria.

The earliest marine horizon in Gabon has yielded an ammonite, the Lower Aptian *Deshayesites consorbinoides* Sinzow according to De Klasz & Gageonnet (1965: 285), although Reyment & Tait (1972) consider it better referred to the Upper Aptian genus *Neodeshayesites*. These beds are succeeded higher up by strata with *Douvilleiceras*, of upper Lower Albian age. Overlying beds have yielded the ammonites *Oxytropidoceras*, *Mortoniceras*, and *Elobiceras*, and probably span much of the remainder of the Albian. The Cap Lopez Formation has been assigned a Cenomanian age on the basis of foraminifers. Turonian strata with *Wrightoceras*, *Bauchioceras*, etc., is well known, although the presence of the Upper Turonian is still in doubt (Reyment & Tait 1972). Coniacian strata with *Peroniceras*, *Gauthiericeras*, and *Barroisiceras* discordantly overlie Turonian rocks (Reyment & Tait 1972). *Texanites* provides evidence of the Santonian, while Upper Campanian is known from the vicinity of Libreville by strata with *Hoplitoplacenticeras* (Reyment 1966: 170).

Records of Aptian from the west coast are based largely on microfossil evidence, although the bivalve *Panis cabrai* (Dartevelle & Freneix) has been used to suggest an Aptian age for strata in Zaïre and Angola. Presumably on the basis of microfossils, Hoppener (1958: 75) recognized a 'transgression aptienne inférieure ou ante aptienne', and a 'transgression aptienne supérieur' from Angola. No ammonites have yet been collected to support this contention.

In Angola (Fig. 3) the earliest undoubted marine beds occur at Dombe Grande, to the south-east of Benguela, and have yielded the ammonites *Douvilleiceras mammillatum inaequinodum* (Quenstedt) and *D. orbignyi* Hyatt (Howarth 1965). The beds immediately above are rich in *Oxytropidoceras* and *Manuaniceras*. These upper Lower Albian–lower Middle Albian beds are characterized by a fauna rich in numbers but poor in species. Unfossiliferous sediments overlying these beds would seem to span the remainder of the Middle Albian and are succeeded by Upper Albian strata with *Mortoniceras*. No ammonites have been recorded from the Middle Albian strata of Angola above beds with *Oxytropidoceras*. Strata presumably of a similar age, at Hanha, the supposed fossil locality of Haas (1942*a*), are also unfossiliferous. Near Hanha,

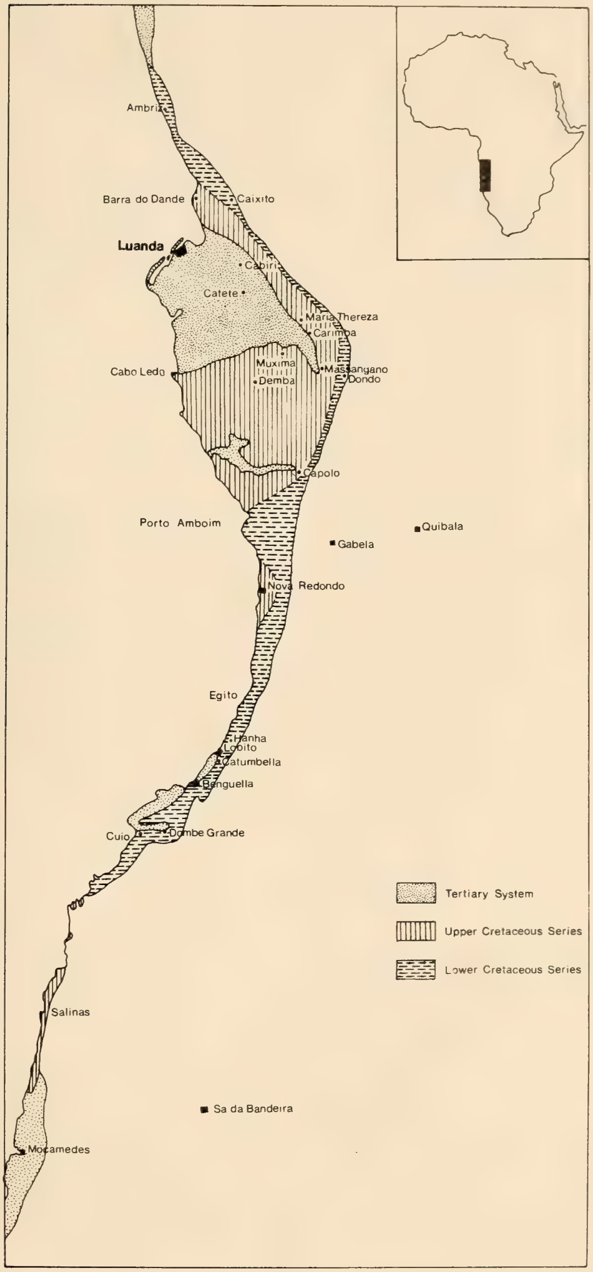

Fig. 3. Locality map showing the distribution of Cretaceous strata in Angola. In part after Mouta & O'Donnell 1933.

however, low Upper Albian strata are rich in *Neokentroceras*, *Dipoloceras*, *Mortoniceras*, etc. The remainder of the Upper Albian in Angola is frequently extremely rich in *Mortoniceras*, *Elobiceras*, *Prohysteroceras*, *Anisoceras* and *Stoliczkaia*. Reyment & Tait (1972), following Howarth (1965), suggested that *Stoliczkaia* was of Lower Cenomanian age in Angola, as did Kennedy (1971). This is wrong. This misconception has arisen from Douvillé's (1931) record of *Stoliczkaia dispar* var. *attenuata* Douvillé from the uppermost Cenomanian of Salinas (Cooper 1972). Further topotype material suggests that this specimen belongs not to this Upper Albian–Lower Cenomanian genus, but should rather be considered the homeomorphous development of some other acanthocerate stock, possibly the early Turonian *Benueites* (W. J. Kennedy, pers. comm.). The uppermost Albian of Angola, as exposed at Egito, is characterized by *Anisoceras perarmatum* Pictet & Campiche, *Stoliczkaia* spp., and mortoniceratids.

At Egito the lowest fossiliferous horizons, resting upon crystalline basement, have yielded *Mortoniceras*, suggesting the beginning of the Upper Albian to have been a period of transgression. As noted by Reyment (1969), uppermost Albian deposits occur closest to the coast, e.g. Egito, Catumbela, suggesting a gradual regression following the early Upper Albian transgression.

Deposits at Salinas indicate the uppermost Cenomanian to have been a period of transgression, yielding the ammonites *Calycoceras naviculare* (Mantell), *Austiniceras dibleyi* Spath, *Pseudocalycoceras angolaense* (Spath), *Sciponoceras gracile* (Shumard), *Kanabiceras septemseriatum* (Cragin) and *Metoicoceras* cf. *whitei* Hyatt. The overlying beds comprise a condensed sequence spanning Turonian and earliest Coniacian times (Cooper 1972), and contain the following ammonite genera: *Mammites*, *Subprionocyclus*, *Damesites*, '*Prionocyclus*', *Hauericeras*, *Baculites*, *Kossmaticeras*, ?*Subtissotia*, *Proplacenticeras*, *Gaudryceras*, *Hypophylloceras*, *Anagaudryceras*, and *Mesopuzosia*. The rich and varied Turonian fauna of Nigeria is not known from Angola. These beds are disconformably overlain by subaerially extruded alkaline volcanics of Upper Coniacian age (Cooper 1972), in turn succeeded by early Santonian marine beds with *Protexanites*, *Texanites*, *Hauericeras* and *Damesites*.

The stratigraphy of the Cuanza basin is at present poorly known. Hoppener (1958) assigned an Upper Aptian age to oolitic limestones near the base of the succession with *Acteonella* aff. *fusiformis*, *Cerithium* cf. *albense*, and *Perna* sp. while a rich Upper Albian fauna is known from Cabo Ledo.

At the beginning of Cenomanian times the sea transgressed in Angola, with *Sharpeiceras laticlavum* (Sharpe) occurring at Cabiri, while in the south of the Cuanza basin, at Novo Redondo, the transgression extended about 20 km inland, the lowest beds yielding the Lower Cenomanian *Mantelliceras* cf. *saxbii* (Sharpe) (Cooper 1973*b*). There was probably a gradual regression until Middle Cenomanian times, since beds with *Turrilites acutus* Passy, *Euomphaloceras cunningtoni* (Sharpe), *Forbesiceras obtectum* (Sharpe), etc., occur at the coast. No higher beds are known from Novo Redondo. Haas (1942*b*) recorded a *Romaniceras* sp. from north of Cabiri, which suggests a Turonian age. Hoppener

(1958) also assigned a Turonian age to *Coilopoceras cacobaensis* sp. nov. (a *nomen nudum* since it was neither figured nor described). Downfaulted strata at Cabo Ledo have yielded an uppermost Turonian fauna with *Prionocyclus* and *Subprionocyclus* (Basse 1963; Matsumoto 1965: 49; Howarth 1968: 225). Of probable Coniacian age is *Proplacenticeras reineckei* (Haughton), while Hoppener (1958) assigned '*Placenticeras*' *fritschi* Hyatt and a *Hemitissotia* sp. to the Coniacian. The occurrence of *Texanites angolanus* Haas and *T. quinquenodosus* (Redtenbacher) to the north of Cabiri provides evidence of the Santonian. A rich, predominantly heteromorph fauna from Barra do Dande suggests an Upper Campanian–Maastrichtian age (Howarth 1965; Antunes & Sornay 1969). Amongst the genera recorded are *Didymoceras*, *Nostoceras*, *Manambolites*, *Solenoceras*, *Axonoceras*, *Polyptychoceras*, and *Sphenodiscus*. Antunes & Sornay (1969) consider these beds, the Barra do Dande Formation, to rest (?) disconformably upon the Pambala Formation which they tentatively dated at Upper Santonian–Lower Campanian on the basis of inoceramids assigned to the *bantu–balticus* group. No ammonites have been collected to support this evidence. The apparent absence of *Hoplitoplacenticeras* at Barra do Dande, a common ammonite in the Upper Campanian fauna of the Egito outlier, suggests that the transgression may have been slightly diachronous, occurring earlier in the south than in the north. From far inland, at Carimba, Haughton (1925) recorded *Nostoceras*, *Didymoceras*, *Menuites*, *Libycoceras*, etc., for which an Upper Campanian–Lower Maastrichtian age appears the most precise dating. A similar age seems the most likely for Haas's (1943) fauna from the Maria Theresa area. A major transgression undoubtedly took place in Angola during Upper Campanian–Maastrichtian times. The base of the transgression is not known from the Cuanza basin, but at Egito is dated at Upper Campanian (*vari* Zone) probably reaching its maximum extent somewhat later. At San Nicolau, a horizon rich in sharks' teeth was assigned to the Maastrichtian (Dartevelle 1942). Cooper (1972), on sedimentalogical grounds, doubted this age determination. In retrospect, however, the occurrence of phosphatic pellets associated with the sharks' teeth suggests the possibility of a non-sequence. Should such a break exist, then these beds possibly represent the base of the late Campanian transgression.

From the Cavaco valley near Benguela, Spath (1951: 124) recorded a 'presumed Campanian' fauna with *Inoceramus langi* Choffat and ammonites tentatively identified as *Hauericeras gardeni* (Baily), *Damesites*, and *Neancyloceras* from clays resting unconformably upon Upper Albian strata.

Haughton (1930) described a small inlier of marine Cretaceous from Bogenfels in South West Africa, from which he recorded the ammonite *Proplacenticeras merenskyi* (Haughton) in association with the oyster *Exogyra* cf. *columba* (Lamarck) (= *Rhynchostreon suborbiculatum* (Lamarck)), these beds being characterized by the abundance of the latter. At Salinas in southern Angola, the uppermost Cenomanian is characterized by the abundance of *Rhynchostreon* cf. *suborbiculatum* (Cooper 1972), which is absent from the overlying beds, nor has it been recorded from the Middle Cenomanian of Novo Redondo. An uppermost Cenomanian age would appear the most likely for the Bogenfels outlier. H. C. Klinger (pers. comm.), who has personally visited the Wanderfeld IV locality of Haughton, considers the Cretaceous fauna to, in all probability, represent remanié, although in this respect the apparent abundance of the diagnostic Cenomanian oyster *R. suborbiculatum* is critical. Haughton (1930) believed these '*Exogyra* beds' to be unconformably overlain by the Senonian with *Protocardia hillana* (Sowerby), *Turritella* (*Zaria*) *bonei* Baily and *T.* (*Haustator*) *meadi* Baily. Together these forms suggest a possible Santonian age.

STRATIGRAPHY OF THE SOUTH COAST

Along the south coast of South Africa (Fig. 4), marine strata at Knysna, long correlated with the Uitenhage Group, have been assigned 'A high Mid-Kimmeridgian age' (Klinger *et al.* 1972) on the basis of the ammonite *Hybonoticeras* aff. *hildebrandti* (Beyrich), while Dingle & Klinger (1972) recorded an ostracode assemblage with strong Callovian affinities. These are the earliest Mesozoic marine sediments to be recorded from South Africa. At Robberg, near Plettenberg Bay, casts of *Megatrigonia conocardiiformis* (Krauss) occur in sandstones of the Enon Formation of the Uitenhage Group, and are probably of Upper Jurassic age, since this species is also known from the Upper Kimmeridgian–Tithonian of Moçambique (Da Silva 1966).

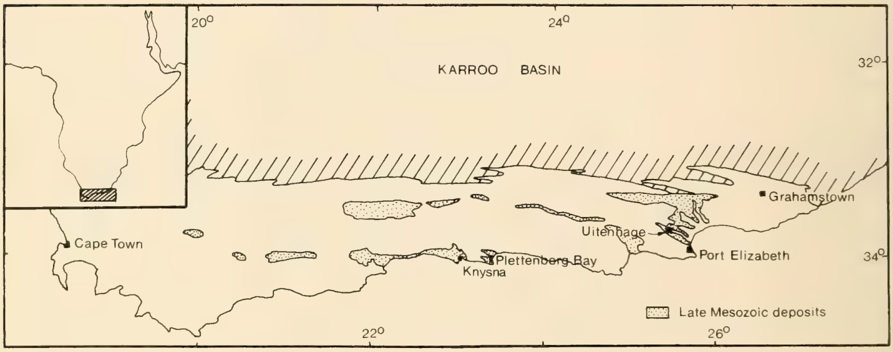

Fig. 4. The distribution of late-Mesozoic strata in the southern Cape. After Geol. Surv. S. Afr. 1970.

To the north of Port Elizabeth, sediments assigned to the Uitenhage Group (Cooper 1973*a*) crop out over wide areas, although it is only the upper portion, the Sundays River Formation, that has yielded ammonites. The cephalopod fauna is characterized by the abundance of species of *Olcostephanus* s.s., together with *Distoloceras*, *Bochianites*, *Eodesmoceras*, *Partschiceras*, ?*Leopoldia*, and *Belemnopsis*. The absence of finely-ribbed forms of *Olcoste-*

phanus, e.g. *O. filosus* (Baumberger), which characterize the Lower Hauterivian of France (Busnardo & Cotillon 1964), and of the subgenus *O.* (*Jeannoticeras*) favours an uppermost Valanginian age for the Uitenhage fauna.

STRATIGRAPHY OF THE EAST COAST

To the south of Port St. Johns, at the Umgazana River mouth (Fig. 5), Cretaceous conglomerates have yielded belemnites, the ammonite *Bochianites* (Du Toit (1954) records the Upper Cretaceous *Baculites*, but this is a misidentification), and the bivalve *Steinmanella* cf. *holubi* (Kitchin). Together these forms favour a correlation with the Uitenhage Group, and an uppermost Valanginian age.

A short distance to the north of Port St. Johns are outcrops of unfossiliferous strata assigned to the Emboyti Formation. Although no marine fossils have yet been recorded, the close lithological similarity with the Umgazana Formation led Du Toit (1954) to suggest a correlation.

The age of the Pondoland Umzamba Formation has long been a source of contention, but Spath (1953) was led to conclude that it represented a condensed sequence. The occurrence of *Pseudoschloenbachia*, *Lewesiceras*, *Texanites*, *Hauericeras*, *Barroisiceras*, *Eulophoceras*, *Forresteria*, *Pseudophyllites*, *Kossmaticeras* (*Natalites*), *Pseudoxybeloceras*, etc., suggests that the condensation may span Upper Coniacian to Lower Campanian times, with the majority of forms Santonian. Gevers & Little (1946) recorded an isolated outlier of Cretaceous, the Itongazi Formation, from between the Umkandandhlovu and Itongazi Rivers in southern Natal. Although no ammonites have yet been recorded, the majority of bivalves and gastropods are also common to the Umzamba Formation, and leave little doubt as to their contemporaneity.

Two quarries at Need's Camp, near East London, have yielded Upper Senonian faunas although no diagnostic forms have been reported. On foraminiferal evidence, McGowran & Moore (1971) have assigned the Lower Quarry an Upper Campanian–Maastrichtian age. The commonest macrofossils are well-preserved sharks' teeth, assigned to *Isurus* and *Carcharias*, the coral *Caryophyllia*, and bryozoans, together with the echinoid *Coptosoma*, the brachiopod *Lacazella*, and the bivalves *Exogyra*, *Neithea*(?) and *Inoceramus*. A similar age has been assigned to the Upper Quarry (King 1972), long considered of Eocene age, also on foraminiferal evidence. Macrofossils from this quarry include teeth of the sharks *Oxyrhina*, *Odontaspis* and *Carcharodon*, the gastropod *Pyropsis*, and the bivalves *Plicatula*, *Panopea* and *Lima*. No ammonites have been recorded from either quarry. Lock (1973), however, considers the Upper Quarry to be Miocene in age, with incorporated Cretaceous and Eocene remanié.

Kennedy *et al.* (1973) have recently described an Upper Santonian–Campanian borehole fauna from Durban, including the following species: *Anagaudryceras subsacya* (Marshall), *Texanites* (*Plesiotexanites*) *stangeri* (Baily),

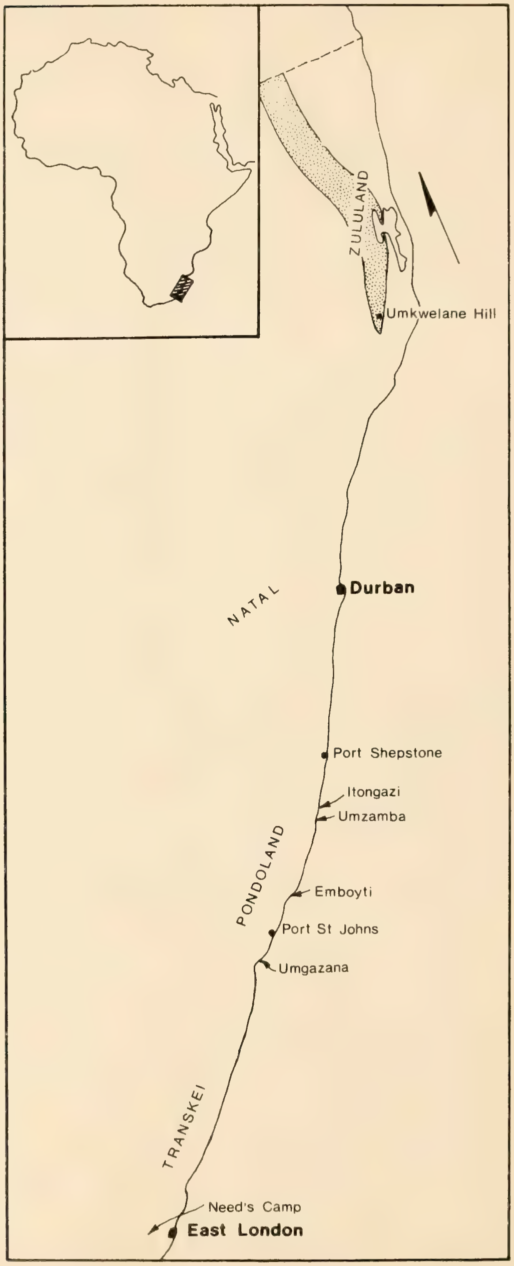

Fig. 5. Locality map showing the Cretaceous exposures along the east coast of South Africa; the Zululand outcrop is stippled. After Geol. Surv. S. Afr. 1970.

Submortoniceras woodsi (Spath), *Hoplitoplacenticeras plasticum* Paulcke, *Hauericeras* cf. *gardeni* (Baily), *Kossmaticeras* (*Natalites*) cf. *acuticostatus* (Spath), etc. These authors considered this fauna to generally resemble that of the Umzamba Formation.

In Zululand the earliest marine outcrops are of Barremian age (W. J. Kennedy and H. C. Klinger, pers. comm.), with the ammonites *Heteroceras*, *Colchidites*, *Phylloceras serum* Oppel, *Eulytoceras phestum* (Matheron), etc. The occurrence of *Tropaeum*, *Australiceras*, *Cheloniceras*, *Acanthohoplites*, and *Diadochoceras* (Haughton *in* Rennie 1936) indicates most of the Aptian to be present. Beds containing *Diadochoceras* are overstepped by strata with *Douvilleiceras mammillatum* (Schlotheim) (Kennedy & Klinger 1971); thereafter deposition appears to have been continuous until the low Upper Cenomanian with *Calycoceras* gr. *naviculare* (Mantell), although after deposition of beds with *Acanthoceras quadratum* Crick, *A*. spp., *Turrilites acutus* Passy, *Calycoceras* spp., *Forbesiceras largilliertianum* (d'Orbigny), etc., the sequence is poorly fossiliferous. These beds are unconformably overlain by Lower Coniacian strata (Kennedy & Klinger 1971) with *Proplacenticeras subkaffrarium* (Spath), *P. umkwelanense* (Etheridge), *P. kaffrarium* (Etheridge), *Kossmaticeras theobaldianum* (Stoliczka), *Bostrychoceras indicum* (Forbes), etc., followed by continuous deposition until the Lower Maastrichtian with *Eubaculites*, *Pachydiscus* (*Neodesmoceras*), and *Saghalinites*. The uppermost Cenomanian and Turonian was a period of non-deposition, the hiatus being represented by a *Lithophaga*-bored hardground.

The earliest recorded marine horizon in Moçambique, at Nacala (Fig. 6), has been dated at Upper Kimmeridgian–Tithonian (Da Silva 1966) on the basis of the bivalves *Trigonia* (*Indotrigonia*) *smeei* auct. and *Astarte krenkeli* Dietrich. A cephalopod from these beds has not yet been described.

Slightly further to the north, at Fernão Veloso, strata with *Olcostephanus schenki* (Oppel) (=*O. baini* (Sharpe)) and *Haploceras* (*Neolissoceras*) cf. *grasianum* (d'Orbigny) (Wray 1915; Spath 1930) provide evidence of the uppermost Valanginian. Strata of a similar age also crop out at Mahiba Hill, west of Port Amélia, from where Newton (1924) recorded fragments of *Lytoceras*, together with the belemnite *Duvalia*. From this same locality, Spath (1930: 134) also records a 'portion of the periphery of a Neocomitid (*Lyticoceras* of the type of *L. regalis* (Bean) or *Neocomites neocomiensis* (d'Orbigny) as figured by Sayn), and the impression of a fragment of the Uitenhage *Bochianites africanus* are decisive and unmistakable'. Neumayr (1885) recorded the Neocomian *Phylloceras semistriatum* (d'Orbigny) from the Moçambique region, an identification subsequently confirmed by Zwierzycki (1913).

Aptian and Albian strata are best known from southern Moçambique (Fig. 7), although exposures are poor and much of the area is capped by younger Neogene deposits.

The best exposures are at Catuane, the so-called Maputoland locality of Spath (1925), where the earliest beds have been assigned to the Upper Aptian

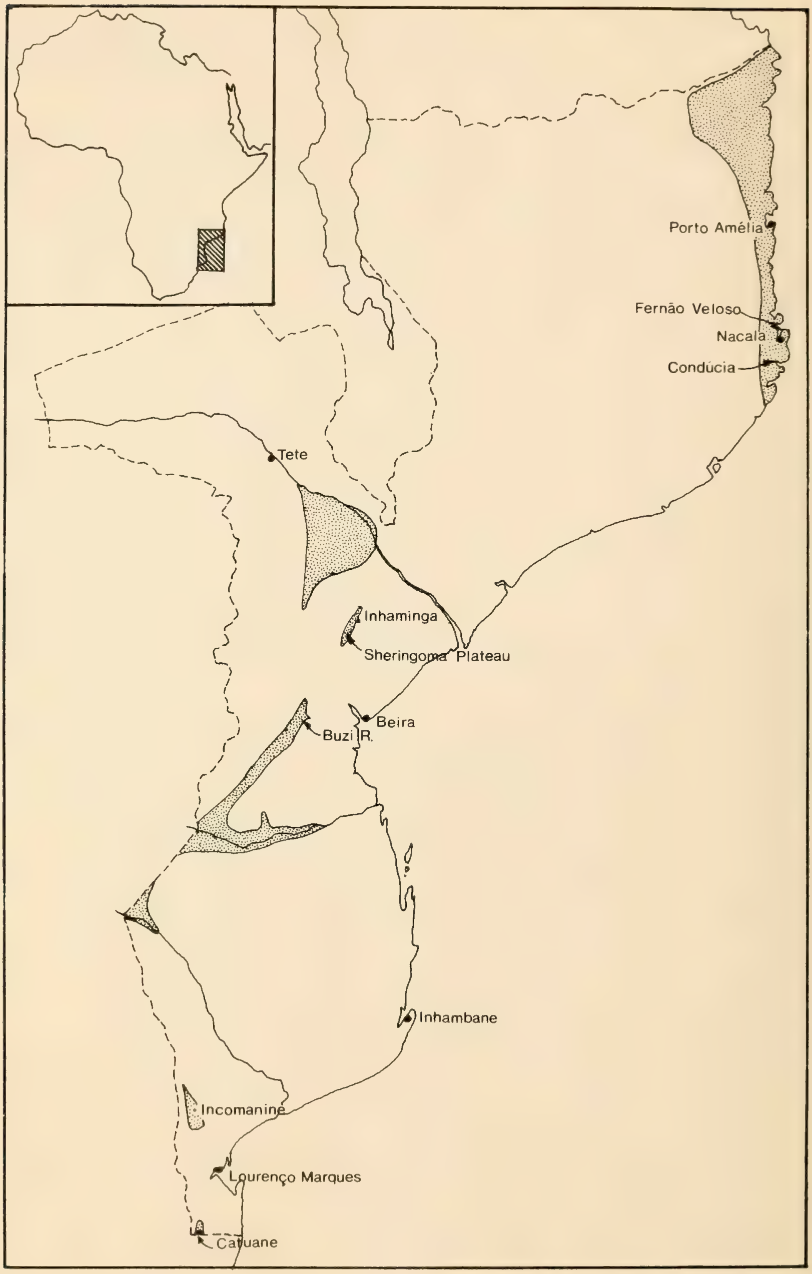

Fig. 6. The distribution of late-Mesozoic strata in Moçambique. Largely after De Freitas 1957.

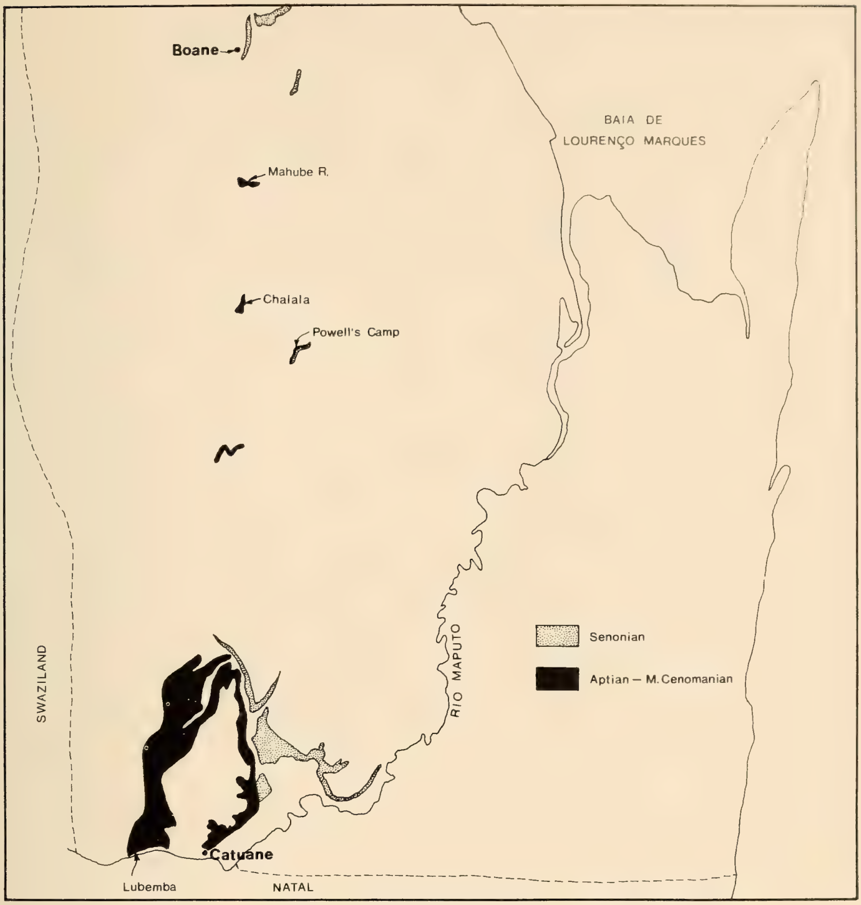

Fig. 7. The Cretaceous exposures of southern Moçambique. After Serviços de Geologia e Minas da Provinçia de Moçambique, 1969.

(Da Silva 1962; Wachendorf 1968). On the farm Lubemba, from where both Da Silva's and Wachendorf's collections came, recent collecting has yielded a rich Lower Aptian (*deshayesi–bowerbanki* Zones) fauna dominated by the abundance of *Cheloniceras* (*Cheloniceras*), together with the genera *Tropaeum*, *Ancyloceras*, '*Neosilesites*', '*Valdedorsella*', *Phylloceras*, *Toxoceratoides*, *Pseudosaynella*, etc. Wachendorf (1968) records *Parahoplites campichei* Pictet & Renevier and *P. melchioris* Anthula from the Maputo River which provide evidence of the Upper Aptian at this locality as well. The occurrence of *Phylloceras* at Lubemba, which Da Silva (1962) thought to resemble *P. velledae* (Michelin), led him to suggest the presence of Albian at this locality. This is incorrect. Recent collecting has shown the *Phylloceras* to be closely associated with *Cheloniceras* (*Cheloniceras*), and thus of Lower Aptian age. No Lower

Albian fossils have yet been recorded from Catuane. The presence of the Middle Albian is indicated by the occurrence of *Oxytropidoceras*, while Spath (1925) has recorded a rich low Upper Albian fauna characterized by the heteromorphs *Anisoceras*, *Labeceras*, and *Myloceras*, together with *Mortoniceras*, *Elobiceras* and *Hysteroceras*. The uppermost Albian (*dispar* Zone) has not been recorded, but its presence is to be suspected. Spath (1925) described *Sharpeiceras florencae* Spath from Maputoland, and thus presumably Catuane. This genus is confined to the Lower Cenomanian. The occurrence of *Trigonarca* cf. *ligeriensis* (d'Orbigny), *Pterotrigonia* (*Scabrotrigonia*) *shepstonei* (Griesbach), and *Amphidonte columba* (Lamarck) (= *Rhynchostreon suborbiculatum* (Lamarck)) from 3 km to the east of Catuane, led Soares & Da Silva (1970) to suggest the presence of the Cenomanian. This is confirmed by the recent collection of a worn fragment of *Calycoceras* from this area. These beds are unconformably overlain by the Mandajene Formation. Amongst 52 species of bivalves and gastropods recorded from this formation (Soares & Da Silva 1970), 31 are common to the Umzamba Formation of Pondoland. Soares & Da Silva (1970: 2) considered the Mandajene Formation to be 'of Santonian–Campanian age, or even Maestrichtian towards Santana de Tinonganine'. Unfortunately, these beds are poor in ammonites. Internal moulds of baculitids were compared with *Baculites capensis* Woods (Soares & Da Silva 1970), while Spath (1925) recorded *Texanites* aff. *soutoni* (Baily) from Maputoland, and presumably, therefore, from this region. The dating of the base of the Senonian transgression in Zululand, of which succession the Catuane deposits are merely a continuation, at Lower Coniacian (Kennedy & Klinger 1971) suggests a similar age for the base of the Mandajene Formation.

Cretaceous strata are again exposed to the west of Porto Henrique, at the renowned Chalala locality (Haughton & Boshoff 1956; Wachendorf 1968), where the presence of *Cheloniceras* (*Cheloniceras*), *Toxoceratoides*, *Aconeceras*, *Acrioceras*, and *Phylloceras* provide evidence of the upper Lower Aptian (*deshayesi–bowerbanki* Zones). Lacey (1961) recorded the presence of *Bostrychoceras* and *Calycoceras* at Chalala, to which he assigned a Cenomanian or Lower Turonian age. The heteromorph fragment was assigned to *Bostrychoceras* on the basis of its rounded whorls and non-tuberculate ribs, while 'The smaller fragment . . . has tubercles and appears to be an indeterminate species of *Calycoceras* which has an age span of Cenomanian to Lower Turonian. Very similar forms such as the Aptian *Cheloniceras* or *Roloboceras* would appear to be excluded by the presence of *Bostrychoceras*, since forms with round whorls and non-tuberculate ribs do not occur before the Cenomanian' (p. 9). These are almost certainly misidentifications since a recent visit to Chalala revealed only friable, unfossiliferous Neogene (?) deposits resting disconformably, with a basal small-pebble conglomerate, upon Lower Aptian strata. Further to the north-east, however, Upper Albian beds with *Mortoniceras*, *Hysteroceras* and *Labeceras* are exposed and are overlapped by Middle Cenomanian strata with *Acanthoceras*.

To the south-east of Porto Henrique, rocks of Cretaceous age are exposed on the Catembe River. Presumably this is the Powell's Camp locality of Spath (1921), from where he described *Aconeceras nisoides* (Sarasin), *Cheloniceras gottschei* (Kilian) and *C. delagoense* (Krenkel), considered to be of Upper Aptian age. There is little doubt that these beds should be correlated with the other similar deposits of southern Moçambique, and be considered of upper Lower Aptian age.

Lower Aptian strata are again exposed along the Mahube River, where the genera *Aconeceras*, *Toxoceratoides*, and *Cheloniceras* were collected. These beds are overlain by the Cenomanian (Soares & Da Silva 1970), characterized by the abundance of *Turrilites costatus* Lamarck, virtually to the exclusion of all else. Soares & Da Silva (1970) have also recorded *Acanthoceras* from this locality. It seems likely that these beds can be correlated with the '*Turrilites costatus* faunal assemblage' of Kennedy (1971), of low Middle Cenomanian age.

Kilian (1902) and Krenkel (1910) both described Aptian fossils collected from 'Delagoa Bay'. No Cretaceous is exposed around Delagoa Bay, and this locality is obviously the regional name applied by the early travellers.

The only other early Cretaceous deposit known from Moçambique is the rich Upper Albian–Cenomanian locality of Conducia, in the north, from where Choffat (1903) recorded *Anagaudryceras sacya* (=*A. choffati* Shimizu), *Mariella bergeri* (=*M. conduciensis* Breistroffer), *Phylloceras semistriatum* d'Orbigny, ?*Baculites* sp., ?*Hamites* sp., *Desmoceras latidorsatum* (Michelin), '*Desmoceras beudanti*' var. *petersoni* Choffat, *Sharpeiceras laticlavium mozambiquense* Choffat, *Calycoceras marquescostae* (Choffat), and *Mortoniceras* cf. *candollei* (Pictet).

Cox (1925) described an entirely new gastropod fauna from Incomanini, to which he assigned an Upper Maastrichtian age, a determination supported by a study of the bivalves (Rennie 1935). The Maastrichtian is also present along the Buzi River and at Sheringoma, from where Crick (1924) has recorded *Eubaculites* cf. *vagina* (Forbes) and the nautiloids *Hercoglossa mazambensis* Crick and *H. sheringomensis* Crick.

The late Mesozoic stratigraphy of Tanzania (Fig. 8) is not well known. 'Nowhere is there good dating below the Callovian, but a considerable part of the Ruvu Beds (q.v.) is apparently Bajocian/Bathonian in age' (Quennell *et al.* 1956: 156). To the east of the Ngarama Plateau sediments assigned to the Mandawa–Mahokondo 'Series' have yielded Upper Oxfordian (*plicatilis*-Zone) ammonites of the genera *Perisphinctes* (*Arisphinctes*), *P.* (*Dichotomosphinctes*), and *Euaspidoceras*. From the same locality the genera *Ptychophylloceras*, *Hecticoceras* (*Sublunuloceras*), *Sindeites*, *Indosphinctes*, *Choffatia*, *Grossouvria*, *Kinkeliniceras*, etc., provide evidence of the Middle and Upper Callovian. The overlying 'Septarian Marls' have been dated at Lower Kimmeridgian (*mutabilis–pseudomutabilis* Zones) by the presence of *Streblites*, *Physodoceras*, *Idoceras*, *Taramelliceras*, *Virgatites*, *Perisphinctes* (*Lithacoceras*), *P.* (*Pachysphinctes*), *Simoceras*, etc. (Quennell *et al.* 1956).

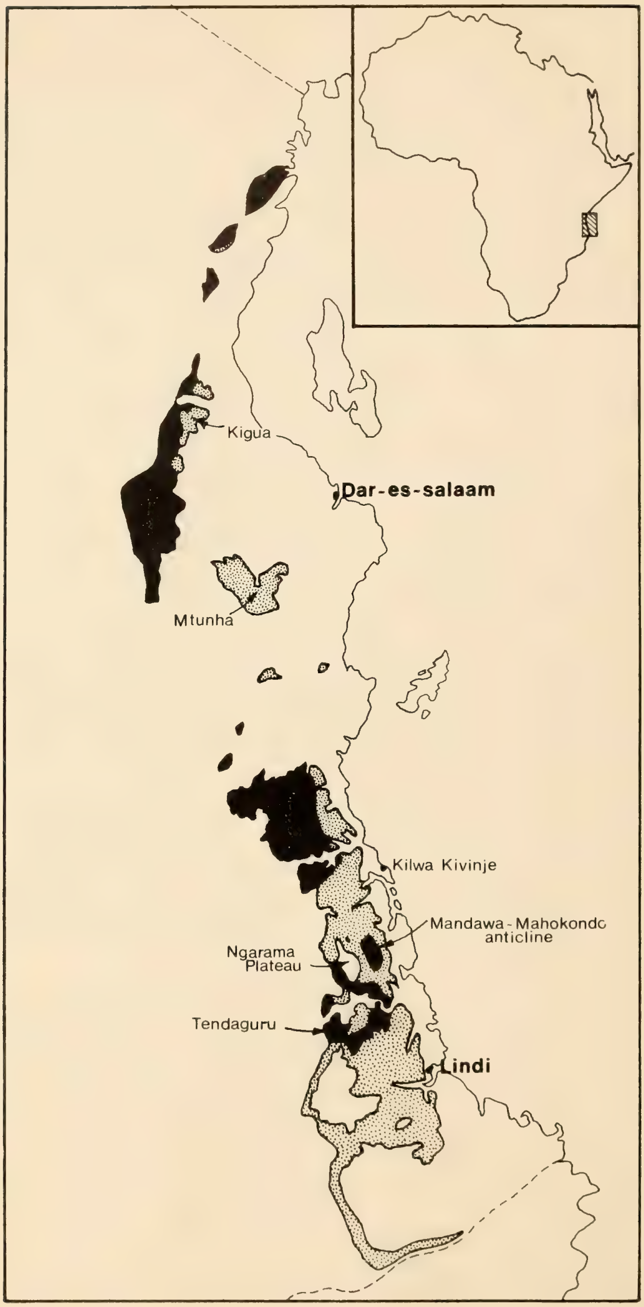

Fig. 8. Distribution of Jurassic (black) and Cretaceous (stippled) strata in Tanzania. After Quennell *et al.* 1956.

From Tendaguru, in the Mbemkuru Valley of southern Tanzania a Lower Tithonian age has been favoured (Quennell *et al.* 1956) for the '*Trigonia smeei* Beds'. The ammonites include *Haploceras*, *Hildoglochiceras*, *Subdichotomoceras*, etc. Above beds with *Trigonia* (*Indotrigonia*) *smeei* (J. Sowerby) occur the non-marine 'Upper Saurian Beds', which are also included in the Jurassic (Quennell *et al.* 1956).

There is an apparent unconformity separating the succeeding '*Trigonia schwarzi* Beds', which have yielded the ammonites *Olcostephanus* (*Olcostephanus*), *O.* (*Jeannoticeras*), *Phylloceras serum* Oppel, *Lytoceras hennigi* Zwierzycki (to which species Zwierzycki (1914) assigned the Moçambique fragments), *Bochianites*, etc. To the north-east of the Mandawa–Mahokondo anticline, Neocomian strata are anticlinally-folded, and unconformably overlain by Aptian strata (Quennell *et al.* 1956). The presence of *Heteroceras*, *Ancyloceras*, *Procheloniceras*, *Cheloniceras* (*Cheloniceras*) *rauffi* (Zwierzycki), and *Diadochoceras nodosocostatum* (d'Orbigny) suggests at least part of the Barremian as well as most of the Aptian to be present, while the occurrence of *Puzosia paronae* Kilian was taken by Zwierzycki (1914) to indicate the Albian. Hennig (1937) recorded *Hysteroceras varicosum* (J. Sowerby), '*Turrilites*' aff. *bergeri* Brongniart, *Phylloceras broilii* Krenkel, *Puzosia kitchini* (Krenkel) (= *Tetragonites kitchini*) and *P. africana* Krenkel *non* Kilian (= *Parasilesites austroafricanus* (Krenkel)) from the Namazatu area, to which he assigned on Albian age. According to Murphy (1967: 36), *Tetragonites kitchini* 'is dated as upper Albian'. Hennig (1937) considered the Cenomanian and Turonian to be absent from Tanzania, although Quennell *et al.* (1956) report Cenomanian strata, presumably based on microfaunal evidence. Furon (1963) considered the Cenomanian to be represented by beds with *Rhynchostreon suborbiculatum* (Lamarck). It seems likely, however, that this species is of an earlier age along the east coast than it is along the west coast. If, as suggested by Reyment & Tait (1972), Africa and Brazil were connected until the early Turonian, then migration of *R. suborbiculatum* during the Cenomanian must have occurred via the eastern shoreline. This species has not yet been recorded from Zululand and does not appear to have migrated this far south by the beginning of the Upper Cenomanian. It is, however, known from the pre-uppermost Cenomanian strata of Catuane (Soares & Da Silva 1970). This suggests that its age in East Africa is either Lower or Middle Cenomanian.

Bate & Bayliss (1973) have recently described the stratigraphy of the Cretaceous succession in the Wami River area, northern Tanzania. The sequence is considered to extend from the Aptian to the Turonian, inclusive. Age determinations are based solely on microfossils, and no macrofossils are reported.

The foraminifers *Rotalipora greenhornensis* (Morrow) and *R. cushmani* (Morrow), together with abundant *Praeglobotruncana delrioensis* (Plummer) were considered diagnostic of the Upper Cenomanian. Middle and Upper Turonian strata are recognized on the basis of the foraminifers *Globotruncana helvetica* Bolli, *G. linneiana* (d'Orbigny), *Hedbergella delrioensis* (Carsey), *Praeglobotruncana stephani* (Gandolfi) and *Clavihedbergella simplex* (Morrow), together with the ostracodes *Cytherelloidea turonica* Bate, *Cytheruna moorei* Bate, *C. lunzangaziensis* Bate, *Curfsina turonica* Bate, *Cythereis luzangaziensis* Bate, *Cytherella afroturonica* Bate, *Akrogmocythere wamiensis* Bate, *Paracypris wamiensis* Bate and *Sphaeroleberis africana* Bate.

It would be most unusual were this succession complete, in view of the fact that breaks in sedimentation are known to exist both to the north and to the south. Consequently, ammonites are needed to corroborate the microfaunal evidence.

The Senonian in Tanzania is known mainly on the basis of microfossils, although Spath (*in* Quennell *et al.* 1956) assigned an ammonite to the genus *Pachydiscus* s.l.

Tavani (1949) considered all horizons from Barremian to Turonian, inclusive, to be present in the Cretaceous deposits of Somalia. No diagnostic Barremian ammonites have yet been recorded, unless *Pseudothurmannia incertus* Tavani is correctly identified, and the presence of this stage is based largely on bivalves and gastropods. Much of the Aptian is present, a rich *Cheloniceras* fauna recording the presence of upper Lower Aptian (*deshayesi–bowerbanki* Zones) strata. The Upper Aptian is represented by beds with *Epicheloniceras subnodosocostatum* (Sinzow), *Parahoplites weissi* Neumayr & Uhlig, *P. rudis* Tavani, *Acanthohoplites* cf. *aschiltaensis* (Anthula), *A. mustahilensis* Tavani, etc. Tavani's (1949) record of *Hypacanthoplites milletianus* (d'Orbigny) suggests the possibility of the presence of uppermost Aptian–lowest Albian (*jacobi–tardefurcata* Zones) strata, beds which appear to be absent from the other stratigraphic sequences of the east coast. This identification should be regarded as tentative, since as pointed out by Casey (1965: 435) 'although it (*Hypacanthoplites milletianus*) is one of the most widely quoted of Albian ammonites, it has been generally wrongly identified'.

Albian strata are known from Bugda Acable where a rich *Douvilleiceras* fauna yielding *D. mammillatum* (Schlotheim), *D. monile* Tavani (*non* J. Sowerby), *D. spinosum* Tavani, *D. benonae* Besairie, *D. variabile* Tavani, and *D. cheloniceratiforme* Tavani indicates the upper Lower Albian (*mammillatum* Zone). Middle Albian strata have yielded *Brancoceras zrissense* Pervinquiére and *B. senequieri* (d'Orbigny), while Owen (1971: 134) considers the occurrence of the endemic lyelliceratid *Somalites vertebralis* Tavani together with *Brancoceras* (although Tavani (1949) records *Somalites* in association with Upper Aptian forms) 'may well indicate the equivalent of the *lyelli* Subzone (Middle Albian)'. The occurrence of a *Hysteroceras* sp. and *Labeceras crassum* Spath provides evidence for the presence of low Upper Albian sediments, although mortoniceratids are still unrecorded.

Tavani (1949: 71) considers the Ferfer Gypseous 'Series' to be of Cenomanian age, as also the base of the Belet Uen 'Series', noting 'qui in Somalia invece il Cenomaniano presenta una estrema scarsità di Ammoniti, rappresentati soltanto da alcuni esemplari appartenenti ai generi *Heterotissotia* and *Placen-*

ticeras'. *Heterotissotia figarii* Greco, known from the Coniacian of Egypt, *H. complanata* Tavani, and *Proplacenticeras tumulicum* (Blandford) are not of Cenomanian age, but are indicative of the Coniacian. Thus, as in Zululand, transgressive Coniacian deposits rest disconformably upon Albian and possibly early Cenomanian strata. According to Furon (1963: 304) the Senonian is known from Somalia by the bivalves *Venericardia beaumonti* (d'Archiac) and '*Exogyra*' *overwegi* von Buch.

THE CRETACEOUS HISTORY OF AFRICA SOUTH OF THE SAHARA

It is now possible to recognize the following Cretaceous history for southern and central Africa. The Africa–South America rift was almost certainly in existence as a rift valley during the late Jurassic–early Cretaceous (Reyment & Tait 1972), with the invading sea reaching Gabon prior to the ?Upper Aptian. Along the east coast rifting began in the north and reached Knysna by at least Upper Jurassic times. With regard to the Jurassic deposits, Klinger *et al.* (1972: 658) noted that 'Occurrences of material comparable to our specimen (*H.* aff. *hildebrandti*) in Kutch and Kenya are thought to be Middle Kimmeridgian (Spath 1927, 1930*a*; Arkell 1956). *Hybonoticeras* also occurs in the Middle Kimmeridgian of Somalia and Ethiopia (Arkell 1956) whilst in Madagascar, where the genus occurs in both Kimmeridgian and Tithonian, the closest comparisons are with forms from Collignon's (1959) Middle Kimmeridgian.' The widespread occurrence of strata of this age along the east coast would seem to date a transgressive episode.

At the end of the Valanginian another marine transgression resulted in the deposits of the Sundays River Formation of the Uitenhage Group (S.E. Cape), the Umgazana and Emboyti Formations of Pondoland, the deposits at Mahibi Hill and Fernão Veloso in Moçambique, and the '*Trigonia schwarzi* Beds' of Tanzania. The Hauterivian appears to have been largely a period of marine regression.

Along the east coast Barremian deposits are known from Somalia and Ethiopia (Furon 1963), Tanzania, Zululand, and also Madagascar. The deposits are generally of limited extent and poorly fossiliferous, although they would seem to date a transgressive episode. Possibly the 'Aptienne inférieure ou ante-aptienne' transgression of Angola (Hoppener 1958) was contemporaneous.

The widespread occurrence of upper Lower Aptian strata in southern Moçambique suggests that this was a period of marine transgression, not Upper Aptian as suggested by Furon (1963: 362), a fact supported by the transgressive Lower Aptian deposits of the Mangoky sector of Madagascar (Haughton 1963: 266). Strata with rich *Cheloniceras* faunas are also known from Somalia and Tanzania, and are undoubtedly related to this transgression. The Upper Aptian was generally regressive, although the sea did not leave the continental margin until the end of the Aptian. In Zululand the Aptian–Albian boundary is a non-sequence (Kennedy & Klinger 1971), as also in Madagascar (Collignon 1963: 2).

By the beginning of the Albian the west coast rift was open at least as far as Nigeria, and the first truly marine transgression, dated at upper Lower Albian (*mammillatum* Zone), affected both east and west coasts, indicating it to have been eustatic in origin. This was followed on both coasts by continuous deposition until the end of the Albian although in Angola, above beds with *Oxytropidoceras*, the Middle Albian is unfossiliferous, suggesting a slight regression. It is thus interesting to note Owen's (1971: 138) remark 'Superficially, it seems that there is in many parts of the Earth a major break in sedimentation, particularly at the top of the Middle Albian. General sedimentation occurred once again in early Upper Albian times.' The *mammillatum* Zone transgression appears locally to have attained its maximum extent only at the beginning of the Middle Albian, e.g. Nigeria, and in the Rodo Valley of Madagascar (Haughton 1963: 264).

At the beginning of the Upper Albian there was a widespread west coast transgression, followed by a slow regression for the remainder of the Albian, with faunal evidence (Reyment & Tait 1972) suggesting West Africa and Brazil to still have been connected during the Middle Albian. Reyment (1969) considers that for a short time during the Upper Albian the South Atlantic appears to have been open along its entire extent. The opening can possibly be related to flooding of the Nigeria–Pernambuco connection by this transgression. The occurrence of Upper Albian strata, apparently overlapping Lower Aptian sediments, near Porto Henrique in Moçambique suggests this transgression was eustatic.

The final break between Africa and South America is believed by Reyment (1969) to have occurred only at the end of the Lower Turonian. With regard to the Cenomanian, Reyment & Tait (1972: 64) wrote 'The role of the Cenomanian in the Atlantic is important. In all cases known to us the deposits of Cenomanian age in the South Atlantic coastal basins accumulated in a regressive sea.'

In Angola, however, Lower Cenomanian strata are known from far inland both at Cabiri and Novo Redondo, while uppermost Albian is not known from these localities. There seems little doubt that in Angola the Lower Cenomanian was a period of transgression. Possibly the somewhat younger beds with *Turrilites costatus* Lamarck along the Mahube River in southern Moçambique are also related to this transgression, resting as they do upon Lower Aptian strata. Following this transgression, there appears to have been a gradual regression until the middle Middle Cenomanian. The highest Cenomanian beds at Novo Redondo in Angola contain *Turrilites acutus*, *Forbesiceras obtectum*, *Euomphaloceras cunningtoni*, etc. A similar regression would appear to have occurred in Nigeria following deposition of beds with *Acanthoceras quadratum* Crick, *Turrilites* sp., *Forbesiceras* sp., etc. In Zululand a rich Middle Cenomanian fauna with *Turrilites acutus*, *Acanthoceras quadratum*, etc., is overlain by poorly fossiliferous sediments of low Upper Cenomanian age, The paucity of fossils in these Upper Cenomanian sediments is possibly related to the slight change in environment caused by this Middle Cenomanian regression. This synchronous

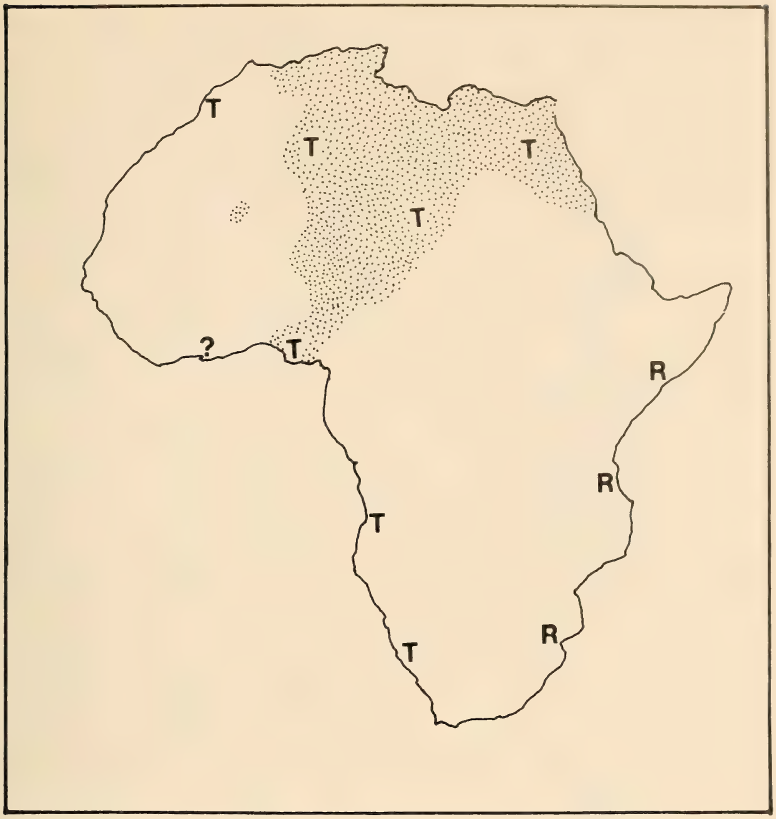

Fig. 9. Africa during uppermost Cenomanian times. T marks the onshore occurrences of uppermost Cenomanian transgressive deposits, with the stippled area indicating the extent of the *Neolobites* transgression in North Africa. R marks Cenomanian localities at which the uppermost Cenomanian is a non-sequence. In part after Reyment 1969.

regression on both sides of the continent suggests the regression was eustatic and not tectonic as suggested by Reyment (1969).

During the uppermost Cenomanian (*Metoicoceras gourdoni* Zone) the sea again transgressed along the west coast, with deposition of the well-known Salinas fauna of Angola, the '*Exogyra* Beds' at Bogenfels in South West Africa, and the beds containing *Metoicoceras* aff. *ornatum* Moreman in Nigeria. This transgression is also indicated by the *Neolobites* faunas of North Africa (Fig. 9). Following this transgression, at San Nicolau in Angola, the sea appears to have remained static, with minimal sediment input (represented by a condensed sequence), until earliest Coniacian times. In Zululand, however, uppermost Cenomanian and Turonian rocks are absent, and low Upper Cenomanian strata are unconformably overlain by Lower Coniacian sediments. The hiatus in Zululand is represented by a hardground, indicating submarine erosion (Rose 1970) and non-deposition. Thus, for almost the exact period represented by the condensed sequence at San Nicolau on the west coast, there was submarine erosion and non-deposition along the east coast. As pointed out by Jenkyns (1971: 330) 'There is an obvious genetic connection between condensed sequences and hardgrounds; condensed sequences are produced by minimal net sedimentation, hardgrounds by nil or negative sedimentation'. Thus, condensation to the west and non-deposition to the east represent slightly differing manifestations of the same regional event.

The absence in Angola of such typical early Turonian forms as *Wrightoceras*, *Bauchioceras*, *Paravascoceras*, *Fagesia*, *Paramammites*, *Nigericeras*, etc., indicates, as suggested by Reyment (1969), that these faunas in West Africa were derived by a transgression from the north, i.e. across the Sahara, the sea only reaching West Africa during the Lower Turonian (Reyment 1971).

At San Nicolau, in Angola, the Turonian–earliest Coniacian condensed sequence is unconformably overlain by alkaline extrusives (Cooper 1972). The absence of pillow-structures together with the unfossiliferous nature of the interbedded sediments suggest subaerial eruption. These volcanics are overlain by a Lower Santonian marine horizon with *Texanites*, *Protexanites*, *Hauericeras*, and *Damesites* (Cooper 1972). Local marginal warping during the Coniacian in Angola can possibly explain the subaerial deposition, the volcanics being related to the tectonic instability of the time. This is supported by the fact that a rich (?)Upper Coniacian fauna with *Peroniceras dravidicum* (Kossmat), *Gauthiericeras margae* (Schlüter), *Barroisiceras haberfellneri* (Hauer), etc., is known from the Ogoové Basin of Gabon (Furon 1963). In South West Africa, Martin (1953) has attributed the reversal of the drainage of the Tsondab Valley, which now flows to the west, as having occurred at some time during the Cretaceous. Possibly it occurred at the beginning of the Santonian.

Along the east coast of South Africa, Kennedy & Klinger (1971: 185) were led to regard the base of the Senonian 'as a diachronous transgressive horizon sedimentation beginning earlier in the north than in the south'. The Mandajene Formation of southern Moçambique can be related to this transgression as can the deposits in Somalia with *Heterotissotia* and *Proplacenticeras*. A similar transgression occurred along the west coast in Gabon, where Coniacian strata rest discordantly upon Turonian rocks (Reyment & Tait 1972), and it would seem to be eustatic in origin.

The Upper Santonian–Lower Campanian appears to have been, in general, a period of regression. Lower Santonian texanitids are common along the west coast, although the only record of Upper Santonian appears to be of a typical *Pseudoschloenbachia* from Cameroun (Reyment *in* Müller 1966: 140). According to Reyment (1966) the Santonian was regressive in the Nigerian basin, while Haughton (1963: 283) noted that the Upper Santonian deposits of the Bas-Zaïre 'are less widespread, a regression having commenced in this substage'. Similarly, Furon (1963: 362) noted that the Santonian was generally

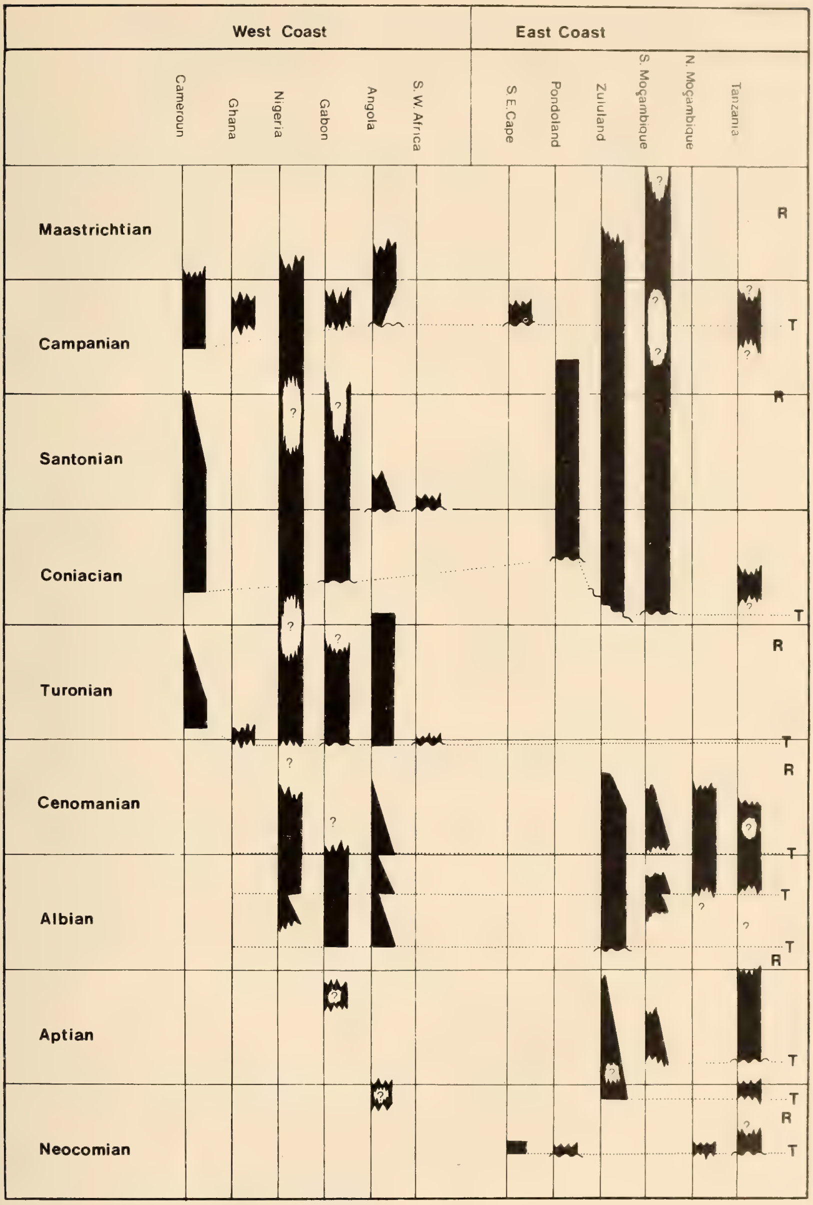

Fig. 10. A comparison of the known Cretaceous stratigraphic sequences along the east and west coasts of south–central Africa. T marks the start of a marine transgression while R marks regressive phases.

regressive in Madagascar. Thus, this regression appears to have been eustatic. The transgressive Lower Santonian of Angola is related to local coastal tilting, and is not thought to be eustatic in origin. The Senonian beds at Bogenfels in South West Africa probably have a similar origin.

A major transgression occurred towards the end of the Campanian, beginning during *Hoplitoplacenticeras vari* Zone times but only reaching its maximum extent somewhat later. The occurrence of similar late Cretaceous outliers at Need's Camp along the east coast, and possibly in the Buzi and Sheringoma regions of southern Moçambique, suggests this transgression was also eustatic. This is supported by the transgressive Upper Campanian deposits of the east coast of Madagascar (Furon 1963).

SUMMARY

A comparison of the Cretaceous sequences along the east and west coasts of southern and central Africa has allowed the recognition of at least nine episodes of marine transgression during the Cretaceous. These are dated at uppermost Valanginian, Barremian, upper Lower Aptian, upper Lower Albian, basal Upper Albian, Lower Cenomanian, uppermost Cenomanian, Lower Coniacian, and Upper Campanian, by the associated ammonite faunas. They appear to best be explained by eustatic changes in sea-level rather than oscillatory tiltings of the African continent.

ACKNOWLEDGEMENTS

I am extremely grateful to Professor R. A. Reyment, Uppsala, for his constructive criticism of the original draft, as well as for many helpful suggestions. Dr W. J. Kennedy and Dr H. C. Klinger critically reviewed the manuscript, whilst also providing me with the latest stratigraphical details of their work in Zululand, for which I am most grateful. Once again Dr Kennedy, with his usual perspicacity, has saved me from a number of errors.

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THE ZOOGEOGRAPHY OF THE SOUTH AFRICAN AVIFAUNA

By

J. M. WINTERBOTTOM

Cape Town Kaapstad

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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R7,50

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1974

ISBN 0 949940 57 7

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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By

J. M. Winterbottom

South African Museum, Cape Town

(With 9 maps and 6 tables)

[*MS accepted 1 November 1973*]

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INTRODUCTION

From the days of P. L. Sclater (1858) and A. R. Wallace (1876), Africa south of the Sahara has been recognized as one of the major faunal regions of the globe. Wallace, in subdividing this, the Ethiopian Region, constituted the area south of the Zambezi and Kunene Rivers as the South African Sub-region and this is the part of the continent dealt with in this paper.

The fauna of any area depends partly on geography and partly on climate, the latter working on animals chiefly through the vegetation. South Africa is the southern extremity of a continent separated on three sides from other land masses by a wide expanse of ocean and on the fourth by deserts. It is generally agreed that the African fauna has most in common with that of the Oriental Region, especially in the case of the forest fauna (De Beaufort 1951); and that the land fauna is sharply divided into forest and non-forest. It is also frequently stated (e.g. by De Beaufort 1951 and Cloudesley-Thompson 1969) that the forest fauna is the older of the two, but I have recently (Winterbottom 1973) given reasons for doubting this. The Ethiopian Region was isolated from the north by the Tethys Sea until the Miocene and by that time had developed its

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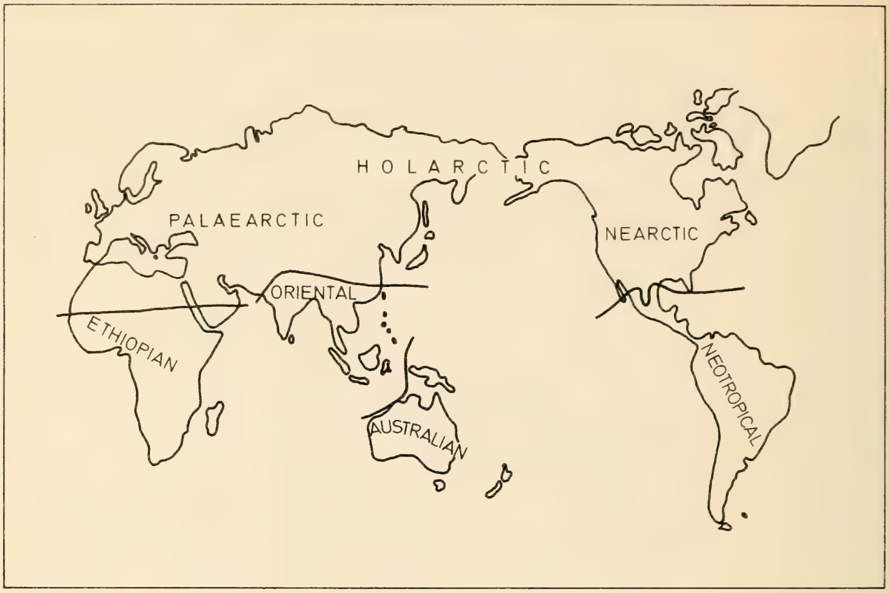

Map 1. Zoogeographical regions of the world.

own individuality. The great expansion of grasslands during this period must have led to considerable speciation (Brodkorb 1960). Although there were times, at least during the Pleistocene, when the present Sahara Desert was inhabitable for a wide range of animals, it is important to note the very considerable climatic differences between north and south. The present bird and butterfly fauna of North America is almost entirely Palaearctic, showing that the Ethiopian elements cannot compete with them in the temperate climate north of the Sahara and the Palaearctic fauna is at a similar disadvantage in the tropical Sudan. It is important to stress this becase the temperate areas south of the Equator are inhabited by a fauna totally distinct from the Palaearctic and clearly derived from the tropical fauna to the north. Much of South Africa has a temperate climate and its fauna, though related to the tropical fauna to the north, has obviously been in existence for a long time, since it has allowed the evolution of at least one distinct family, the Promeropidae, and a number of distinct genera, such as *Geocolaptes* and *Chaetops*. Hall (1970) finds that the African passerine fauna is relatively rich, as compared with the Oriental and Palaearctic, in fruit-eaters (8%) and seed-eaters (24%). The South African avifauna, with only 2% fruit-eaters and 18% seed-eaters, is markedly less so than the African fauna as a whole.

As with the temperate fauna in the extreme south-west, the desert fauna of South Africa has long been isolated, or almost isolated, from the deserts to the north, and genera such as *Namibornis*, *Lanioturdus* and *Philetairus* have evolved there. The genus *Namibornis* is a particularly enlightening one in this respect, since it appears to be intermediate between the Turdine genus *Cercomela* and the Muscicapine genus *Melaenornis*, so its ancestors must have arrived before the groups diverged (Jensen & Jensen 1971). The question of links with the north-eastern desert area of Somaliland is discussed below.

Of the endemic South African species, the majority, as might be expected, have their nearest relatives either in South Africa itself or in adjoining areas to the north. Apart from the southwest–northeast species pairs, which are discussed below, there are five whose nearest relatives occur in the Palaearctic and about 14 whose affinities are obscure but which have obviously had a long history in South Africa.

In summary, the terrestrial avifauna of South Africa contains 6% of species which are found in other zoogeographical regions, 33% which range widely over the whole Ethiopian Region, and 34% which occur also in East as well as South Africa (Table 1). Among the non-passerines, the figures for the first two of these categories are higher than in the passerines, being 12% for cosmopolitan and 40% for Ethiopian species.

Table 1

Geographical affinities of breeding South African land birds (percentages)

	Cosmo-politan	Ethio-pian	South & East Africa	S.W.–N.E. only	West Central Africa	South Africa	Total No. of Species
Non-passerine	12	40	32	½	0	15	225
Passerine	2	28	35	2	2	31	241
All species	6	33	34	1	1	25	466

If we consider the South African terrestrial avifauna at the generic level, we need to use wider categories. These, as used in Table 2, are: Cosmopolitan, being genera represented in both Old and New Worlds and in at least four

Table 2

Geographical affinities of genera of breeding South African land birds (percentages)

	Cosmopolitan	Old World	Pan-tropical	Ethiopian and Oriental	Ethiopian and Palaearctic	Ethiopian and Neotropical	Ethiopian	South and East Africa	South Africa	Total No. of Genera
Non-passerine	22	22	3	1	4	1	44	0	1	96
Passerine	7	16	0	6	4	0	58	2	7	120
All species	13	19	1	4	4	1	53	1	5	216

zoogeographical regions; Old World, being genera represented in at least three of the four regions of the Old World; Pan-tropical Old World, genera represented in the Ethiopian, Oriental and Australian Regions but not in the Palaearctic; Ethiopian and Oriental; Ethiopian and Palaearctic; Ethiopian and Neotropical; Ethiopian, being genera widespread in the Region; South and East African; and South African. As at the species level, the percentage with Cosmopolitan affinities is markedly higher among the non-passerines than among the passerines (to obtain a comparable total to the Cosmopolitan species in Table 1, the first six columns of Table 2 should be summed); but the percentage of Ethiopian genera is much higher than the percentage of Ethiopian species (as might be expected) and is higher in the passerines than in the non-passerines; but the percentage of South African genera is small, confirming the view that South Africa does not merit rank as a major division of the Ethiopian Region.

Udvardy (1969) analyses the tendency for species to change their range by the use of what he terms 'dynamic potential'. Species with distribution limits in the area being considered constitute the Intrinsic Dynamic Potential; species which moved their limit during the time period considered represent the Realized Dynamic Potential and those which did not move, the Unrealized Dynamic Potential. He gives a table to show this in respect of the Carpathian Basin, 1860–1960. However, the application of this type of analysis to South Africa is complicated by several factors:

(i) Lying as it does at the end of a continent, all the breeding species on the South African list (665, excluding sea birds) find their limits in the area, so that the Intrinsic Dynamic Potential is 665.

(ii) Since the area is bounded by the sea on the west, south and east, all movement must be from the north.

(iii) Owing to the great size of the area, it is necessary to introduce an additional category to those used by Udvardy, namely species advancing in the area. There are 8 of these for the period 1900–1970; 9 are receding; 3 are sporadic breeders; and 1 is newly arrived, giving a Realized Dynamic Potential of 21 (Carpathian Basin, 37). This suggests that the South African avifauna as a whole is rather static.

In discussing the zoogeography of southern Africa, it is essential to realize that five different patterns are involved, since the barriers which are effective for one set of species are the areas of distribution of others. This is obvious if we consider the sea and the land, the former being a barrier to land birds and the latter to sea birds. The five patterns here mentioned are:

(i) oceanic birds;
(ii) coastal birds;
(iii) freshwater birds;
(iv) montane birds;
(v) the rest.

These patterns become more and more complicated as one proceeds from (i) to (v) and, especially in (v), it is exceedingly difficult to disentangle geographical from ecological factors. Since (v) is much the most widespread and has excited greatest comment, I propose to deal with these patterns in the reverse order to that listed above.

LOWLAND AND PLATEAU

The lowland and plateau areas, which occupy most of the land of South Africa, vary in their climate and vegetation from the bare sand-dunes of the Namib Desert* to the close woodland of the *Baikiaea* 'mutemwa' of western Rhodesia and north-east Botswana and the sometimes impenetrable thickets of the macchia vegetation of the southern Cape. The geographical distribution of avian species within this complex is therefore naturally very varied. I made a list of 51 species which are found throughout, or almost throughout, South Africa; but it by no means follows that because a species has a wide geographical range, it also has a wide ecological tolerance. Of the 51 species mentioned above, three do not appear in any of the lists of dominant or abundant species in the different habitats considered by Winterbottom (1972*b*). Those with much the widest ecological tolerance appear to be the two doves *Streptopelia capicola* and *S. senegalensis*, followed by *Lanius collaris*, *Dicrurus adsimilis*, *Ploceus velatus* and *Sylvietta rufescens*. Generally speaking, therefore, even species very widespread geographically are limited to one or a few habitats and occur only in them, so that, in effect, their distribution is patchy rather than general.

There have been a number of attempts to deal with the zoogeography of South Africa. Wallace (1876) made it one of the four sub-regions into which he divided the Ethiopian Region; Chapin (1932) divided it into the South West Arid and South East Veld Districts, the boundaries of each of which he extended rather beyond Wallace's (and our) limits of the Zambezi and Kunene. Bowen (1933) produced an entirely different arrangement. Unfortunately, his maps are on so small a scale that it is extremely difficult to make out the boundaries he proposes; within our area, however, he recognizes two zones, four 'climates' and five districts. Of these, his Rhodesian Savanna District is roughly equivalent to our South Central Highlands; his Southeast Veldt to our Macchia and Highveld, with the southern Karoo and Rhodesian plateau added; and his East African Lowland to the two northern divisions of our East African Coastal. In the south-west, he divides the area in two by a line running down the centre of Damaraland—an impossible division: but if more realistically adjusted, this may be taken as marking the boundary between our South Temperate and South West Arid Districts. He leaves the coastal areas from Beira to Cape Town as a transition zone, 'in which both Tropical and Subtropical Zone species may occur'.

Moreau (1952) divided South Africa in three, splitting off the south-west

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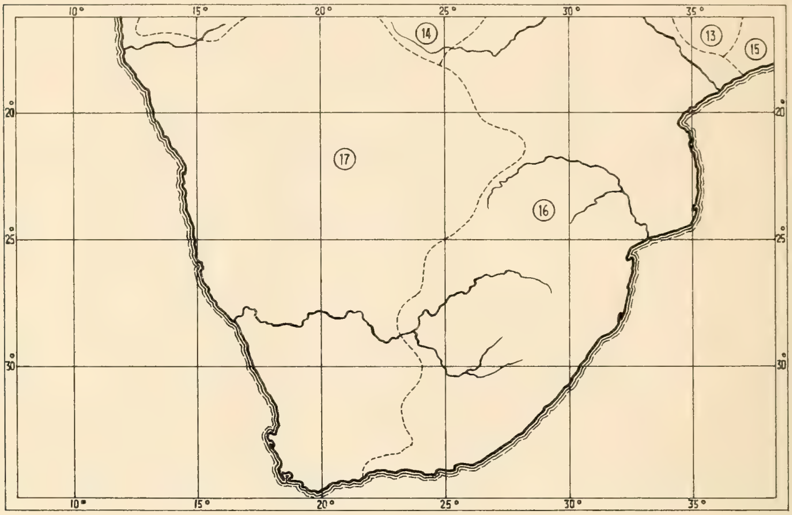
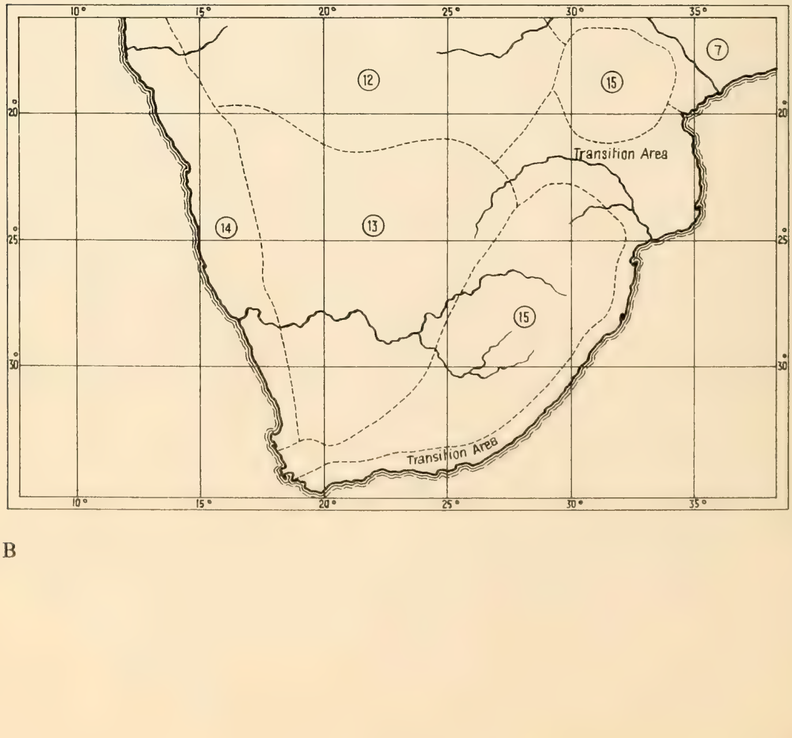
* Places mentioned in the text are shown on Map 9.

Map 2. Zoogeographical divisions of South Africa according to A. Chapin; B. Bowen; C. Moreau; D. Poynton.



Map A



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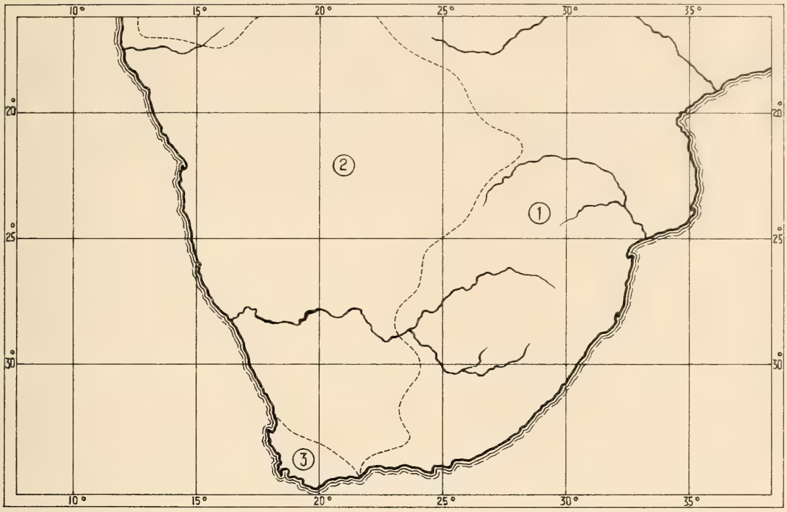

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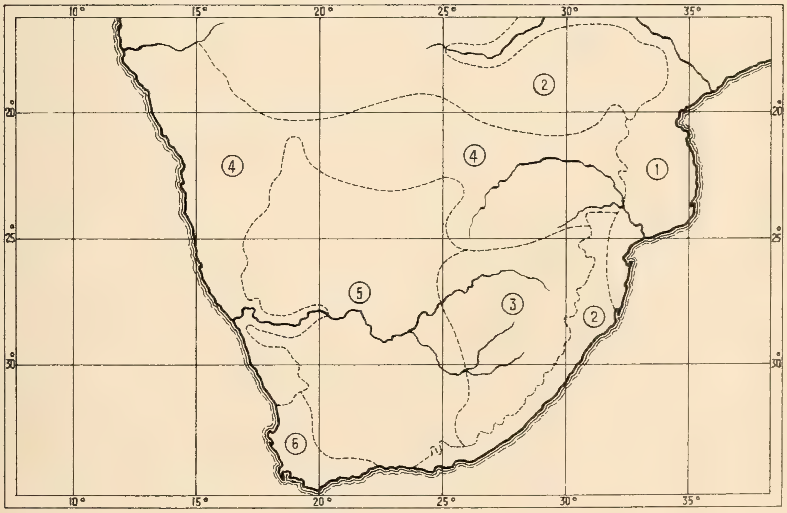


Map D

Cape from the rest and uniting Chapin's South East Veld with vast areas the to north as a Southern Savanna District. Winterbottom (1959) removed the Highveld grasslands from Chapin's South East Veld to his South West Arid and divided the rest of that district between his Rhodesian Highlands and East African Coastal Districts. Poynton (1964), like Moreau, divided off the south-western Cape; he put most of the South West Arid into a Temperate Western and the rest into a Subtropical Arid, except for the extreme north, where he proposed a division running right across from Ovamboland to the eastern Highlands of Rhodesia as a Subtropical Moist. He retained the highveld as a Temperate Eastern. The coastal strip north to about St. Lucia, with the Transvaal and Swaziland lowveld, made up a Subtropical Moist and the rest of the low country on the east, including the Zambezi valley to the Victoria Falls, was his Tropical division. Poynton's divisions were based on the distribution of the Amphibia. His distinction of the South-West Cape is entirely justifiable in respect of its amphibian fauna but not for birds and mammals.

One further attempt needs to be discussed. Roberts (1940) proposed to divide South Africa into 21 'small regions', a concept which was taken over, with minor modifications, by McLachlan & Liversidge (1957, 1970). These, although not so called by the authors, are, in effect, 'biotic provinces' as developed by Dice (1952). Of the divisions they propose, their Southern and Eastern Evergreen Forest, Southern and South-western Cape and a few others have some validity, though the detailed evidence on which they are based has never been published. Many of the others, however, have no biological reality at all and the birds which the authors cite, when they do list any, do not support their conclusions. Thus the only bird listed for the Little Karoo is *Circus maurus*, which I personally have never seen there, though no doubt it does occur; but which is found all over their Southern and South-western Cape, their Karoo, their Eastern Grassveld and much of their Great Namaqualand and Highveld Grassveld. They cite four species for their Thornveld Kalahari, *Turdoides bicolor*, *Laniarius atrococcineus*, *Mirafra africanoides* and *Erythropygia paena*, all of which occur almost throughout the South West Arid District. Among their Damaraland species, they list *Tockus bradfieldi*, whose range barely reaches the extreme north-east of this division but extends across the northern parts of their Sandveld Kalahari and Ngamiland to western Rhodesia and which they also list as the sole species for their Rhodesian Woodlands.

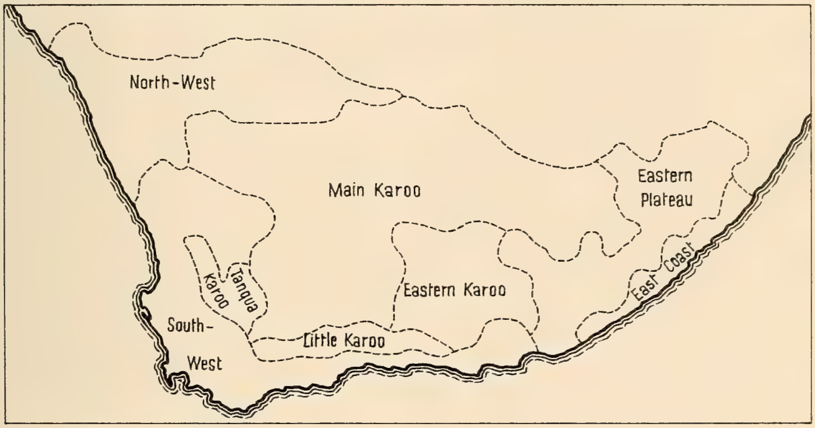
As far as can be judged from their map, Durban and St. Lucia are in their Eastern Littoral, Ndumu in their Eastern Lowveld and Lourenço Marques in their Eastern Tropical Littoral. Analysis of the avifaunas of these places shows that St. Lucia has much more in common with Ndumu than with Durban; that Lourenço Marques has an avifauna as similar to that of Ndumu as St. Lucia's is; and that the avifauna of Durban has more in common with that of East London than with that of St. Lucia. This is in accord with the suggestions made below, which would group St. Lucia and Ndumu with Lourenço Marques in one sub-district of the East African Coastal District and Durban and East

London in another, with the area between St. Lucia and Durban as a transitional zone.

In an endeavour to apply McLachlan & Liversidge's concepts more closely, to see what would come of a detailed analysis, I drew up a list of species not distributed all over South Africa; listed those which occurred in each magisterial district (and sub-district in the western Cape, as set out in Winterbottom, 1968*b*) in the Cape Province south of the Orange River; and compared the lists for each district so obtained with those of all the adjoining districts, using the Co-efficient of Community as defined by the formula:

$$\frac{c}{n_1 + n_2 - c} \times 100$$

where c is the number of species in common and n_1, n_2 are the numbers in the smaller and larger faunas respectively. Lines were then drawn through district boundaries where the co-efficients indicated faunal change. The results are shown in Map 3 and differ considerably from McLachlan & Liversidge's 'small regions' for the same area. The number of species used in the analysis was 329.



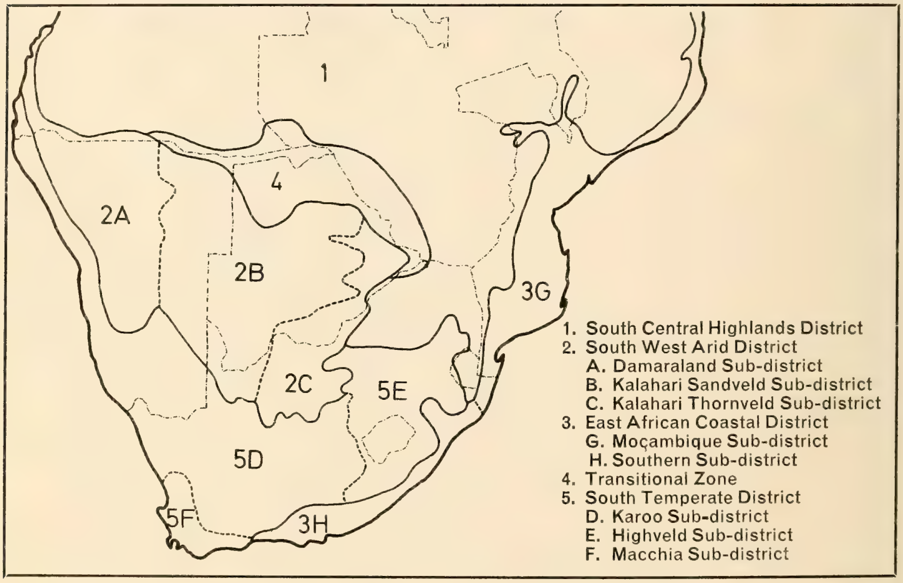
Map 3. Avifaunal areas of the Cape Province south of the Orange River.

Apart from the unsatisfactory nature of the actual divisions proposed, the whole concept of biotic provinces, like those of life zones and faunal groups (on the second of which, see Winterbottom 1965), is an attempt to find a way out of the difficulties—very real difficulties—of the classical method of regions and districts. Unfortunately, however, these methods, at least to my mind, produce results even less satisfactory than those they were designed to supersede.

It will be realized from what has been said above and what follows, that modern zoogeographers reject Wallace's division of South Africa as a distinct sub-region of the Ethiopian Region and that the boundaries of the various zoogeographical areas which have been proposed do not coincide with the Zambezi and Kunene Rivers at any point. For various reasons, the present paper is primarily concerned with Wallace's sub-region, to which about 130 species are restricted, but it is appreciated that all those subdivisions which reach the Zambezi or Kunene continue north of the rivers, though the avifauna of these northern areas is not considered in detail here.

My own views on the zoogeographical subdivisions in South Africa are shown in Map 4. It will be seen that there are four districts (apart from montane forest) partly or wholly within the area: the South Central Highlands, the East African Coastal, the South West Arid and the Southern Temperate; plus an extended Transitional Zone between the first and third. Comments on, and justification of, the establishment of these districts follow.

The most fundamental pattern in bird distribution in South Africa is the dichotomy between east and west. I have listed 106 species whose distribution does not extend west of the main eastern escarpment, though some of them occur in the montane forest of that area; and 103 whose distribution, at least north of Port Elizabeth, does not extend east of the same escarpment. There is a third common pattern, that of species which occur in the north, often south to the Limpopo or even the northern Transvaal, in the west but extend further south, into Natal and sometimes the eastern Cape, in the east. These are species whose main centre of distribution lies north of our limits.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2. South West Arid District
A. Damaraland Sub-district
B. Kalahari Sandveld Sub-district
C. Kalahari Thornveld Sub-district
3. East African Coastal District
G. Moçambique Sub-district
H. Southern Sub-district
4. Transitional Zone
5. South Temperate District
D. Karoo Sub-district
E. Highveld Sub-district
F. Macchia Sub-district

Map 4. Zoogeographical regions of South Africa.

Although the discussion in this paper is mainly of the geographical distribution patterns, these must obviously be influenced by ecological conditions. They are not discussed in detail here since that has already been done elsewhere (Winterbottom 1972*a*). Hall & Moreau (1970) say 'It is the distribution of vegetation which governs the geographical lines along which speciation has taken place'. But things are by no means as simple as this, as perusal of my ecological paper will show. In fact, Hall & Moreau use as their base map (as does Moreau 1966) a map produced by Cooke (1962) which is by no means always suitable to show the relations between bird and plant distribution. This is particularly the case with the 'Dry Woodland, etc., mostly Acacia', which is extended east to include the highveld grasslands and thus obscures the ecological preferences of over 40 species.

It is nevertheless important for zoogeographical purposes to know something of the major habitats available to birds in each of the areas delimited in Map 4.

1. *South Central Highlands*

Most of the area is covered with *Brachystegia* woodland (miombo), fairly close woodland of rather small, deciduous trees with grass ground cover. There are also stretches of *Baikiaea* woodland of somewhat similar character and of mopane woodland, more open and with more scattered grass. In Rhodesia, and also in extra-limital Zambia, there are stretches of open grassland with scattered *Acacia* trees.

2. *East African Coast*

Chiefly scrub *Acacia* woodland, with patches of temperate forest.

3. *South West Arid*

Chiefly *Acacia* woodland on sand, with more open grassland in the south-east.

4. *Southern Temperate*

Macchia—bushes of *Protea*, *Erica*, etc.—in the extreme south; Karoo—small, scattered bushes; with bare gravel and sand-dunes in the Namib; Highveld—open grassland.

The climatic vicissitudes of the Pleistocene must have changed the distribution of these vegetation types; but it would not appear to have eliminated or drastically reduced or seriously fragmented any of them. Clark (1967) produces a map showing the vegetation at 50% of the present rainfall; and while it is unlikely that the rainfall decreased simultaneously over the whole continent, Clark's map does support the conclusion that an arid corridor linked, or almost linked, the South West Arid District with the Somali Arid, perhaps several times. This explains the curious relationships between the avifaunas of the two districts. The following species are found in both, but not in the intervening areas:

Poliohierax semitorquatus, *Eupodotis ruficrista*, *Mirafra africanoides*, *Turdoides melanops*, *Nectarinia mariquensis*, *Ploceus rubigenosus*, *Passer motitensis*, *Bubalornis albirostris*, *Estrilda erythronotus* and *Amadina fasciata*.

A number of other species (e.g. *Pterocles gutturalis*, *Francolinus sephaena*) have been excluded because they range rather far beyond South West Arid limits. In addition, there are over 20 cases of closely-related pairs of species, some of which some systematists regard as conspecific. Yet the presence of endemic genera in each area suggests that there was only a limited exchange of fauna. The question has been more fully discussed elsewhere and an analysis of the avifaunas of the South West Arid and Southern Temperate Districts (Winterbottom 1972*c*) shows that of the 90 characteristic species, 34 are specifically identical or closely allied to species otherwise found in the Somali Arid District; 24 are nearly related to species which occur further east in South Africa; and the 32 remaining forms are peculiar to these districts and their origins are in many cases obscure. Several of them, however, suggest more than one invasion from the north and/or radiation in the south-west. The Pleistocene arid periods, when the Kalahari sands were blown deep into the Congo basin, have left south-west arid relicts further north—the populations of *Certhilauda albofasciata* in Angola and Tanzania are examples.

While the temperate forest faunas have been repeatedly isolated and then joined again, a process which facilitates and accelerates speciation, this has not been the case with the non-forest habitats. Keast (1972) has pointed out that in Australia the desert is central and as it expanded and contracted, the fauna of the more mesic habitats were alternately driven into 'refuges' and then brought together again, while the desert fauna itself remained undivided and was presented with little opportunity for speciation. In Africa, however, it is the deserts which are peripheral. Contact between the northern deserts and those of the south-west has been minimal and the faunas are decidedly different (Winterbottom 1972*c*). The two existing deserts in the south-west are separated by the somewhat less arid Karoo and are decidedly different in character. The Namib, as shown by its remarkable flora and arthropod and herpetological fauna, is very old; but it appears to have always been of very restricted area. The Kalahari, by contrast, has undoubtedly fluctuated greatly in size. At the height of arid periods, Kalahari-type vegetation apparently extended right across the continent in the Limpopo basin to the Indian Ocean and northward deep into the Congo basin. At such times, the south-western portions were under a much more severe desert regime than they are today. On the other hand, during pluvial periods, the northern and north-western parts of the present desert would have been bushveld. Nevertheless, at no time would either desert have been fragmented.

The avifauna of the Namib contains several endemic bird species; that of the Kalahari does not—its avifauna is merely an impoverished version of that of the *Acacia* steppe further west.

EAST AFRICAN COASTAL DISTRICT

The two major groups of east and west mentioned above characterize what Winterbottom (1959) defined as the South West Arid and South East Coastal Districts. The latter has two sub-districts within our limits, besides a third north of the Rovuma River in East Africa. The division between the other sub-districts may be drawn at St. Lucia, south-west of which there is a rapid fall-off in tropical species; but the area from St. Lucia to Durban is regarded as a transitional zone between the two; and, as will be seen below, the fixing of the boundary is by no means as simple as some authors have assumed, the whole of the southern part being, as it were, a subtraction zone at the end of the tropical belt further north.

Of the characteristic species of the northern of the two sub-districts, two drop out between Ndumu and St. Lucia, nine between St. Lucia and Durban and 12 between Durban and Port St. Johns (these figures are based on Pooley & Dixon (1966) for Ndumu; Natal Parks Board (undated) for St. Lucia; Lawson (1971) for Durban; and McCulloch, Skead & Winterbottom (1970) for Port St. Johns). The 23 tropical species which drop out along this stretch of coastal plain are:

Guttera edouardi, Tauraco porphyriolophus, Ceuthmochares aereus, Eurystomus glaucurus, Stactolaema leucotis, Pogoniulus bilineatus, Campethera abingoni, Smithornis capensis, Andropadus flaviventris, Nicator chloris, Cossypha heuglini, Erythropygia quadrivirgata, Apalis ruddi, Batis fratrum, Platysteira peltata, Malaconotus quadricolor, Prionops scopifrons, Nectarinia neergaardi, N. bifasciata, N. senegalensis, Zosterops senegalensis, Hypargos margaritatus and *Lagonosticta senegala.*

Ekman's Index of faunal change* $\frac{A + B}{C}$, where A is the number of species in the larger fauna, B in the smaller fauna and C of the species in common, is largest (2,7) between Port Alfred and the Tsitsikama and lies between 2,2 and 2,4 between other localities from Ndumu to Swellendam, at the south-west boundary of the district (Map 5).

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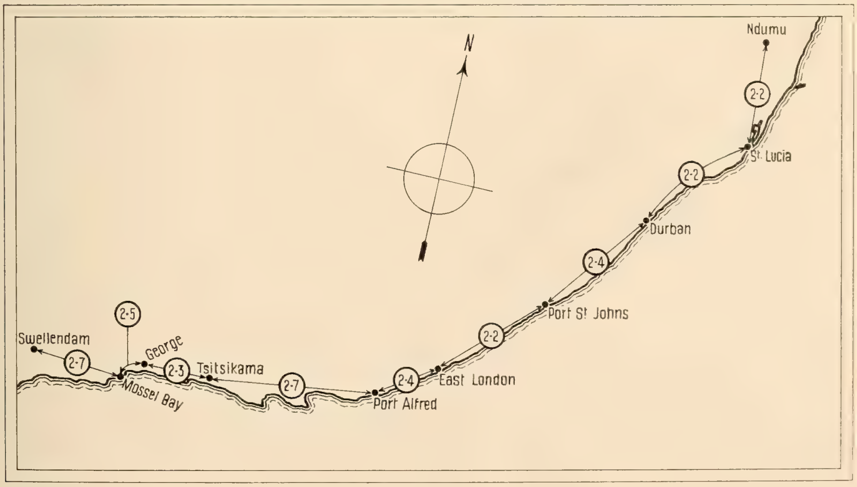
* Ekman's Index is actually much more complicated than this and I have not attempted to assess his 'positive zoogeographical values'—see Udvardy (1969) for a discussion.



Map 5. Ekman's Index along the south-east coast.

Another method of measuring faunal change is by Schilder's Index (Udvardy 1969). The Percentage Occurrence Index derived from this, in respect of the East African Coastal District between Ndumu and Swellendam would consist, for each station, of the number of species present at Ndumu but not at Swellendam in each plus the number of species present at Swellendam absent from the other stations, expressed as a percentage of the Ndumu figure (which will, obviously, be 100%). The full list is:

Ndumu	100
St. Lucia	92
Durban	79
Port St. Johns	52
East London	47
Port Alfred	31
Tsitsikama	24
George	19
Mossel Bay	11
Swellendam	0

It will be seen that the biggest faunal change is between Durban and Port St. Johns (27%), not between Port Alfred and Tstisikama, and is high too between St. Lucia and Durban. This agrees better with the suggestion that the area between St. Lucia and Durban is a transition zone between the two sub-districts.

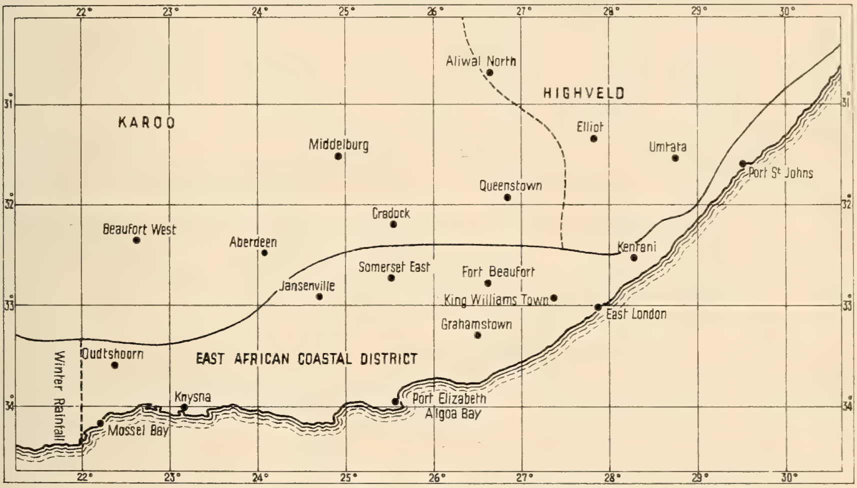
As mentioned above, there are many species which, although confined to the east south of the Limpopo, extend westwards across the Rhodesian plateau into Zambia and Angola and are, in fact, inhabitants of the South Central Highlands District as well as of the Eastern Coastal. To what extent, therefore, are we justified in keeping the two separate?

The avifauna of the Rhodesian plateau, omitting water birds, non-breeding migrants, montane forest and montane grassland birds and species which just impinge on it from the South West Arid District, I have calculated (from Smithers, Irwin & Paterson 1957) to consist of 296 species. The avifauna of the East African Coastal area from the Save River to Natal I count as 324 species (based on Pinto 1953, and Clancey 1953). Of these, 236 species occur in both. This gives a Coefficient of Community of 61,4. This is a little below the figure usually taken to indicate identity of fauna (Hagmeier & Stults 1964); and in view of the fact that both Pinto and Clancey cover areas some distance west of the East African Coastal District, so that some South Central Highlands birds may have crept into the Coastal list, the distinction between the two districts is justified. The following key species characterize the East African Coastal District, those in brackets being extralimital to South Africa:

Francolinus rovumae, *Poicephalus cryptoxanthus*, (*Tauraco fischeri*), *Halcyon senegaloides*, *Pogoniulus pusillus*, *P. simplex*, *Campethera notata*, (*Turdoides squamulatus*), *Lioptilus nigricapillus*, *Phyllastrephus debilis*, *Andropadus importunus*, *Turdus fischeri*, *Cossypha dichroa*, *Erythropygia signata*, *E. quadrivirgata*, *Sheppardia gunningi*, *Bradypterus barratti*, *B. sylvaticus*, *Apalis ruddi*, (*Erythro-*

cercus holochlorus), *Batis fratrum*, *Erythrocercus livingstonei*, (*Anthus melindae*), (*A. sokokoensis*), (*Macronyx aurantigula*), *Tchagra tchagra*, *Malaconotus quadricolor*, *Prionops scopifrons*, *Lamprotornis corruscus*, (*Spreo fischeri*), (*Nectarinia pembae*), *N. neergaardi*, *N. veroxii*, *Anthreptes reichenowi*, (*A. neglectus*), *Ploceus subaureus*, (*P. golandi*), (*Euplectes nigroventris*), *Hypargos margaritatus Serinus scotops* and *S. citrinipectus*.

As I have shown elsewhere (Winterbottom 1965), there are two centres of species concentration in the East African Coastal District, one in Mozambique and the other opposite Zanzibar and Pemba; though further exploration of the coastal belt in northern Mozambique may show that this bipolarity is due to imperfect knowledge.



Map 6. Lines of Maximal Faunal Change, south-east Cape.

The boundary of the South East Coastal District at its southern extremity is based on a map (Map 6) showing the range-limits of 234 species by 1° squares. This somewhat rough-and-ready method simplifies an exceedingly complicated pattern. The northward bulge in the boundary between 24° and 27°E. is due to the extension of the distribution of many coastal birds into the lush vegetation of the inland mountains, while Karoo birds infiltrate south in the drier valleys between the ranges. In the square 32–33°S., 26–27°E. this phenomenon is particularly marked, for 125 species find their limits in this square.

SOUTH CENTRAL HIGHLANDS DISTRICT

Where my proposals differ most radically from those of previous workers is in the extent of the South Central Highlands District. Benson & Irwin (1966), in their fine paper on the *Brachystegia* avifauna, tentatively suggest that the whole extent of this woodland might be regarded as forming a zoogeographical unit, which would fuse Chapin's Rhodesian Highlands and his East African Highlands Districts (except that part of the latter north of the Equator) and would add the Rhodesian plateau to the district too. I am in complete agreement with these suggestions, which, indeed, I had recommended in part over 30 years ago (Winterbottom 1942), but it will be noted that I have (i) carried the zoogeographical districts across the Luangwa and Zambezi rifts, where the vegetation is dominated by the mopane *Colophospermum mopane*; and (ii) taken it further south to include the middle Limpopo valley and the Transvaal and Swaziland lowveld, some of which is also dominated by *Colophospermum mopane* and the rest by *Acacia* and other trees.

The differences in the avifauna east and west of the Lebombo mountains have been commented on by Vincent (1951); and my views on the northern and eastern Transvaal have already been expressed (Winterbottom 1962). The question of the mopane avifauna is not discussed in any detail by Benson & Irwin, to whose paper it would have been irrelevant.

That the avifauna of mopane differs significantly from that of *Brachystegia* is, I think, clear and the differences are discussed elsewhere (Winterbottom 1972*a*, 1972*b*). However, no such thorough investigation of the mopane avifauna as that of Benson & Irwin for *Brachystegia* has ever been made. Benson & Irwin list 96 *Brachystegia* species from the Rhodesian area of that woodland, of which 19 do not occur south of the Limpopo. A further 13 species are listed as of limited distribution in *Brachystegia* and of these 12 occur south of the Limpopo and the other is confined to the area north of the Zambezi. There are therefore altogether 109 species typical of Rhodesian *Brachystegia*, of which 90 (83%) extend beyond that belt into South Africa. These include 17 of the 29 species confined to *Brachystegia* where that occurs. Benson & Irwin exclude raptors from their list; and these would swell the number of species common to *Brachystegia* and the area south of the Limpopo and to the mopane woodland further north to a significant extent.

I believe, therefore, that the inclusion of the mopane areas of the Zambezi and Luangwa valleys and of the southern lowveld within the South Central Highlands District is justified.

Excluding forms extra-limital to our area, such as *Seicercus laurae*, *Cisticola dambo* and *Myioparus boehmi*, species confined to the South Central Highlands, or virtually so, are as follows:

Centropus cupreicaudus, *Coracias spatulata*, *Stactolaema whytii*, *Campethera bennetti*, *Pinarornis plumosus*, *Monticola angolensis*, *Thamnolaea arnoti*, *Camaroptera stierlingi*, *Cisticola pipiens*, *Lanius souzae*, *Parus rufiventris*, *Lamprotornis acuticaudus*, *Ploceus olivaceiceps* and *Serinus mennelli*.

It will be noted that by no means all of these are birds of the *Brachystegia*.

WESTERN DISTRICTS

As already indicated, Chapin (1923) placed all that part of South Africa west of the highveld grasslands and the Rhodesian plateau in a single district, the South West Arid; Moreau (1952) split off the macchia areas of the extreme south-west; and Winterbottom (1959) extended Chapin's original district to include the highveld as well as the macchia. There are some 37 species which are widespread in this extended South West Arid District and virtually confined to it: *Melierax canorus, Francolinus levaillantoides, Otis kori, O. ludwigii, Eupodotis afra, Cursorius rufus, Pterocles namaqua, Colius colius, Mirafra apiata, M. sabota, Certhilauda albofasciata, Calandrella starki, C. conirostris, Eremopterix verticalis, Hirundo spilodera, Anthoscopus minutus, Pycnonotus nigricans, Parisoma subcaeruleum, Melaenornis silens, M. infuscatus, Batis pririt, Oenanthe monticola, Cercomela schlegelii, Myrmecocichla formicivora, Prinia flavicans, P. pectoralis, Laniarius atrococcineus, Malaconotus zeylonus, Onychognathus nabouroup, Lamprotornis nitens, Nectarinia fusca, Sporopipes squamifrons, Amadina erythrocephala, Uraeginthus granatinus, Serinus flaviventris, Emberiza impetuani* and *E. capensis.*

Table 3

Coefficients of Community: western districts

	Winter Rainfall	Karoo	Highveld	Damaraland	Sandveld Kalahari	Kalahari Woodland
Winter Rainfall . .	—	51	55	25	24	34
Karoo	51	—	57	46	46	32
Highveld	55	57	—	52	46	46
Damaraland . . .	25	46	52	—	60	60
Sandveld Kalahari .	24	46	46	60	—	51
Kalahari Woodland .	30	32	46	60	51	—

Nevertheless, there are differences between one part of this area and another and Winterbottom (1969) accordingly divided it into six sub-districts: Winter Rainfall; Karoo; Highveld; Damaraland; Sandveld Kalahari; and Kalahari Woodland. Later, Winterbottom (1970) suggested that these sub-districts fell into two groups and proposed to separate the first three as a Southern Temperate District.

If we analyse the faunas of these various sub-districts, using the Coefficient of Community and omitting aquatic forms, we find that the group consisting of the Winter Rainfall, Karoo and Highveld have coefficients of 51–57 *inter se*; and the Damaraland and two Kalahari divisions have coefficients of 51–60 *inter se.* Except in the case of Damaraland and the Highveld, between which the coefficient is 52, the coefficient between divisions in different groups in no case exceeds 46 (Table 3). Inspection of Table 3 also shows that the Winter Rainfall area is the most distinct (average coefficient 37) and the Highveld least (average coefficient 52,8).

The anomalously high coefficient between Damaraland and the Highveld is due to the fact that each contains a higher percentage of species of wide range in the Ethiopian Region further north but which do not penetrate as far south as the other subdivisions. McLachlan & Liversidge (1970) say of the Sandveld

Kalahari 'perhaps mainly characterised by its lack of birds'; and it is, in fact, merely an impoverished version of the Damaraland fauna, 95% of its species being recorded from Damaraland too.

Cooke (1962) produces a map showing the hypothetical vegetation at 50–60% of the present rainfall. This shows that the Karoo would be divided into a northern and a southern section by a broad corridor of desert across Great Namaqualand, linking the Namib with the Kalahari. I can find no trace of this in the present bird distribution, and it is odd that, of the list of Namib birds given by Willoughby & Cade (1967), not a single one is confined to the Namib and Kalahari; all are either Namib endemics or widely distributed in other parts of the south-west.

In commenting on his previous suggestions, Chapin (1932) remarked, with his usual perspicacity, that his treatment of South Africa was the least satisfactory part of his classification and that more districts might be needed. If we split the enlarged South West Arid District on the lines proposed above and confirmed by the figures in Table 3, we find three genera confined to the restricted South West Arid and four to the Southern Temperate; with one (*Philetairus*) occurring in parts of each. The endemic genera and species of these two districts are:

South West Arid District

Genera: *Namibornis*
Achaetops
Lanioturdus

Doubtful genus: *Aethocichla*

Species: *Francolinus hartlaubi*
*F. adspersus**
Pterocles burchelli
Poicephalus rueppellii
Agapornis roseicollis
Tockus monteiri
*T. bradfieldi**
Mirafra chuana
Turdoides bicolor
T. gymnogenys
Monticola brevipes
Melaenornis mariquensis
Erythropygia paena
Namibornis herero
Achaetops pycnopygius
Lanioturdus torquatus
Laniarius atrococcineus
*Lamprotornis australis**
Vidua regia

In addition, the Southwest–Northeast species *Poliohierax semitorquatus*, *Turdoides melanops*, *Bubalornis albirostris*, *Estrilda erythronotos* and *Ploceus rubiginosus* are confined to this district in South Africa.

Southern Temperate District

Genera: *Geocolaptes*
Calendula
Chaetops
Stenostira

Doubtful genera: *Sigelus*
Euryptila

Species: *Circus maurus*
Francolinus africanus
F. capensis
*Bubo capensis**
Eupodotis vigorsii
Merops apiaster
Geocolaptes olivaceus
Certhilauda curvirostris
C. albescens
Calendula magnirostris
Eremopterix australis
Hirundo albigularis
Macronyx capensis
Chaetops frenatus
Parisoma lyardi
*Melaenornis silens**
Stenostira scita
Cercomela sinuata
C. tractrac
Monticola rupestris
M. explorator
Erythropygia coryphaeus
Cisticola subruficapilla
Prinia maculosa
P. substriata
*Tchagra tchagra**
Spreo bicolor
*Ploceus capensis**
Serinus tottus
S. alario
S. albogularis

Species marked * extend somewhat beyond the boundaries of the district in which they are listed. Not included in the Southern Temperate list are species confined, or virtually confined, to one sub-district (18 in all). These will be discussed later. *Merops apiaster*, of course, also breeds in the Palaearctic and is widespread in Africa as a non-breeding migrant; and we might have added *Ciconia ciconia* to the Southern Temperate list, since it does the same, though its breeding population in South Africa is very small.

Table 4

Zoogeographical affinities: western species

District	% of Avifauna					
	Cosmo-politan	Ethiopian	S. & E. African	S.W.–N.E. only	S.W. Endemic	Sectional Endemic
South West Arid . .	11	37	24	3	16	9
Southern Temperate .	11	33	23	3	16	14

In Table 4, the zoogeographical affinities of the avifauna are set out. Six categories have been used: Cosmopolitan, being species found in the Ethiopian and one or more other regions; Ethiopian, being species of wide distribution within that region; South and East African, being species of wide distribution in South and East Africa but not extending to West Africa; Southwest–Northeast only, being species found in south-western and north-eastern Africa but not in the intervening area; South West endemics, which are found in both western districts; and sectional endemics, found in only one or the other of these two districts. It will be seen that the Southern Temperate District contains a higher percentage of endemics and a lower percentage of Ethiopian species than the South West Arid.

Moreau (1966) analyses faunas in five categories: A, aquatic birds; B, raptorial and scavenging birds; C, game and other ground birds; D, other non-passerines; and E, passerines. Omitting category A, the results for the two districts of the south-west area are set out in Table 5. It will be seen that the two present rather different faunas, the first having more ground birds and passerines and the second more raptors and 'other non-passerines'. That the Southern Temperate should have more ground birds is to be expected in view of the small extent of woodland in its area, nearly all of which is more or less open country. Moreau (1966) has drawn attention to the relative decline in group D species as one proceeds further from the Equator; and the Southern Temperate District is almost wholly extra-tropical, whereas much of the South West Arid is within the tropics, so that the difference in Group D is to be expected. Moreau attributes the decline to the relative paucity of large insects, which are a major food requirement for many Group D species, in more temperate regions. Many of these species are also dependent on tree-holes for nest-sites and these, too, are in shorter supply further from the Equator.

Table 5

Numbers and percentages of species by categories

District	No. of Species					Percentage			
	B	C	D	E	Total	B	C	D	E
Southern Temperate . .	29	41	44	165	279	10	15	16	59
South West Arid . . .	45	31	58	154	288	16	11	20	53
Somali Arid	39	24	68	161	292	13	8	23	55
Sudanese Arid	42	29	74	163	308	14	9	24	53

I have included in Table 5 an analysis on similar lines of the avifaunas of Chapin's Somali Arid and Sudanese Arid Districts. These figures show that the South West Arid avifauna is intermediate between these wholly tropical faunas and that of the Southern Temperate District in respect of group D. All three of the more tropical faunas have fewer passerines and ground birds but more raptors than the southern fauna. The relationships between these arid faunas are more fully discussed elsewhere (Winterbottom 1972*c*).

Moreau (1966) uses the same classification as that discussed above to analyse the faunas of 'sample-areas' in certain vegetation types. He gives one example for the South West Arid District. This relates to *Acacia* woodland in the central Kalahari and, as may be seen from Table 6, represents a decidedly impoverished fauna when compared with Damaraland areas further west, even with Valencia, on the borders of the Namib (Kemp & Kemp 1972); or with the

Kalahari Gemsbok National Park further south (Prozesky & Haagner 1962), but not with the miserable fauna recorded from Tsabong (Pianka & Huey 1971). Moreau explains that the poor fauna of his Kalahari sample is partly because it contains only the birds present in the dry season and therefore omits all breeding migrants. However, this cannot account for Pianka & Huey's results.

Table 6

Numbers of species in sample areas, South West Arid District

Locality	Latitude	Longitude	C	D	E	Total
Central Kalahari . . .	*c.* 24°S.	*c.* 23°E.	12	16	43	71
Sturmfeld	21°38′S.	18°51′E.	14	28	58	100
Sissekab.	19°22′S.	17°11′E.	16	38	65	119
Otjivasandu.	19°12′S.	14°28′E.	14	22	61	97
Gemsbok Park	26–27°S.	20–21°E.	25	20	66	111
Valencia.	23°10′S.	16°25′E.	9	23	46	78
Tsabong.	26°08′S.	22°28′E.	6	7	19	32

Similar lists for 12 Karoo localities in the Southern Temperate District have an average for groups C–E species of 45,6, with a range of 32–61. They are markedly inferior to the South West areas in all groups. Six Winter Rainfall localities have an average for the same groups of 48,3, with a range of 38–59, suggesting a similar type of avifauna to that of the Karoo. A single sample from the Highveld (based on Boddam-Whetham 1965) has 88 species in groups C–E, including 22 in group D; and is thus intermediate between the Karoo areas and those of the South West Arid. Thus the Southern Temperate District in general contains rather fewer species as a whole than the South West Arid (Table 5) and decidedly fewer in any one locality.

The inter-relations of the various sub-districts of the South West Arid and Southern Temperate Districts have been discussed above and also elsewhere (Winterbottom 1968*b*, 1971*a*). However, some comments may be made on the Southern Temperate sub-districts and particularly on the Highveld.

Winter Rainfall Area

There are six indigenous species in the Winter Rainfall area: *Anthus crenatus*, *Pycnonotus capensis*, *Bradypterus victorini*, *Promerops cafer*, *Nectarinia violacea* and *Serinus leucopterus*. It is, as remarked above, the most distinct of the three Southern Temperate sub-districts and only 13 of the widespread south-western birds (p. 125) but 25 of the Southern Temperate endemics occur as breeding species. That this avifauna is primarily derived from areas further north and east, especially the Karoo and the South Eastern Coastal District, is shown by the fact that an analysis of the terrestrial birds in Moreau's groups C, D and E gives the proportions of one indigenous species to five found also in other South Temperate divisions to 11 widespread in South Africa. In view of the marked individuality of the lower vertebrates and of the plants of this area, some explanation would seem to be needed; and I have suggested (Winterbottom

1968*c*) that the most important factors may 'have been the same ones, whatever they are, which have been responsible for the reduction in size of the avifauna as one proceeds from low latitudes to high; with the relatively lesser ecological diversity of the vegetation type as a contributing factor'.

Karoo

Five species are endemic to the Karoo; *Alaemon grayi*, *A. burra*, *Calandrella sclateri*, *Camaroptera subcinnamomea* and *Eremomela gregalis.* Of these, *A. grayi* is confined to the Namib. No less than 35 of the 37 south-western endemics occur widely on the Karoo; and 26 of the Southern Temperate endemics.

Highveld

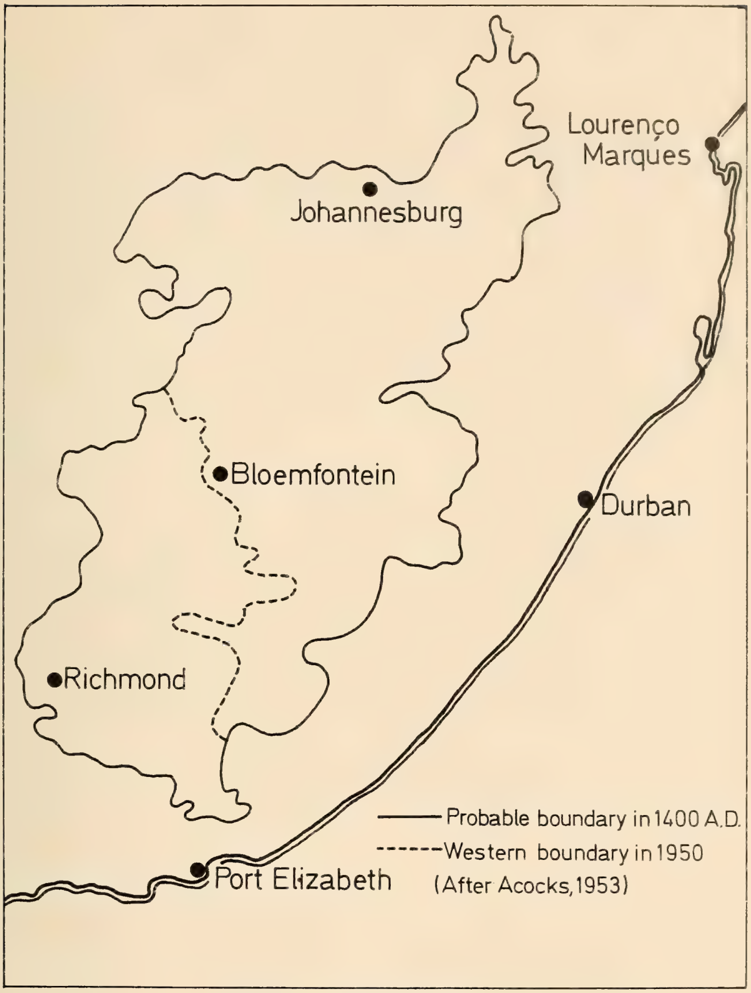
The highveld grasslands of South Africa have their closest, and virtually their only, counterpart in the rest of the Ethiopian Region in the high grasslands of Ethiopia, from which they are cut off by some 2 500 miles (4 000 km) of intervening tropical and subtropical vegetation. Nevertheless, out of 143 terrestrial species listed by Urban & Brown (1971) for the highland grasslands of Ethiopia, 77 (54 %) are recorded for the Orange Free State (Van der Plaat 1961) and/or Lesotho (Jacot-Guillarmod 1963).

In considering the avifauna of the highveld and its affinities, two recent man-made changes must be taken into consideration. The first, in point of beginning, is the progressive degradation of the grassveld and its replacement by Karoo as a consequence of 300 years of over-grazing and other agricultural malpractices. Acocks (1953), our chief authority on such matters, believes that the Karoo has advanced at least 2° eastward in the last 450 years (Map 7). The original westward boundary of the grassveld coincides with a climatic change from temperate to tropical. It is necessary to bear this in mind since a number of typical highveld birds, such as *Eupodotis caerulescens*, *Anthropoides paradisea*, *Hirundo spilodera* and the nominate race of *Certhilauda albofasciata*, still inhabit this former grassveld area. This is in significant contrast to the Karoo enclave in the Breede River valley, which is natural Karoo and where, for instance, the subspecies of *Serinus flaviventris* and *Certhilauda curvirostris* are the Karoo forms *quintoni* and *gilli* respectively and not the subspecies of the surrounding macchia, *flaviventris* and *curvirostris.*

The second change has been the considerable planting of trees, mostly aliens, round houses and as wind-breaks, which has led to the invasion of, or at least increase in numbers in, this originally treeless area by arboreal species previously rare or absent (see, e.g., Freer 1965).

Both these changes affect attempts to assess the composition of the highveld avifauna, the first by suggesting that some highveld endemics or near-endemics range to a considerable distance beyond the grassveld; and the second by suggesting that a number of woodland species inhabit the highveld too.

A full list of the characteristic birds of the grasslands will be found in Winterbottom (1972*a*) but for zoogeographical purposes, there are six species confined, or almost confined, to this division. They are:



Map 7. Highveld Grassland.

Geronticus calvus, *Eupodotis caerulescens*, *Calandrella fringillaris*, *Mirafra ruddi*, *Anthus chloris* and *Promerops gurneyi*.

The last of these is not an inhabitant of grassland but of *Protea* bush and it reappears in the *Protea* bush of the eastern highlands of Rhodesia. It is obviously closely related to *P. cafer* of the Winter Rainfall area, with which it occasionally hybridises in the King Williams' Town area, where the two species are sympatric (Skead 1964).

TRANSITIONAL ZONE

This comprises a mosaic of *Baikiaea*, *Acacia* and mopane woodland, open grassland, flood plains and swamps. Examination of the ranges of individual species show that many characteristic birds of the South Central Highlands extend into this zone, where they meet other forms characteristic of the South West Arid. This is, for instance, the area of overlap between *Pycnonotus barbatus* and *P. nigricans*; *Melierax metabates* and *M. canorus*; *Tockus alboterminatus* and *T. bradfieldi*; *Mirafra rufocinnamomea* and *M. apiata*; *Turdoides jardeneii* and *T. melanops*; *Prinia subflava* and *P. flavicans*; *Laniarius aethiopicus* and *L. bicolor*: though some of these species pairs are ecologically separated. It marks the southern limit in the west of such species as *Streptopelia semitorquata*, *Poicephalus robustus*, *Macrodipteryx vexillarius*, *Merops pusillus*, *Andropadus flaviventris* and *Monticola angolensis*; and the northern limit of, for example, *Laniarius atrococcineus*, *Lamprotornis australis*, *Bubalornis albirostris*, *Pterocles namaqua* and *P. burchelli*. The mixed nature of its avifauna is apparent from these examples. Smithers (1964) divides the Botswana part into several areas, but the Coefficients of Community between these range from 60 to 75, indicating identity of fauna.

MONTANE

Chapin (1932) pointed out that the montane areas of the Ethiopian Region, scattered and fragmented as they are, formed a zoogeographical unit with a distribution pattern quite distinct from that of the lower country. He accordingly grouped them together as a Humid Montane Province, dividing it into two districts, a Cameroon Montane District and an East African Montane District. He did not, however, include any montane areas south of the Zambezi in this province.

Moreau (1966) remarks of the montane forests south of the Zambezi that they contain 'less than half [the number of species] . . . occupying the montane forests of Malawi' and dismisses them from his discussion in two brief paragraphs. Closer investigation, however, suggests that Moreau was exaggerating. I compiled from Benson (1953) a list of 91 species inhabiting montane forests in Malawi; of this list, 68 species (75%) are recorded from forest in Rhodesia and/or southern Mozambique and 58 (64%) from south of the Limpopo. One or two species (e.g. *Pogonocichla swynnertoni* for Rhodesia and *Cossypha dichroa* for South Africa) must be added to obtain the total avifaunas of these southern forests but it is clear that at least the Rhodesian montane forests and that of Gorongoza must be included in the same zoogeographical division as the montane forests further north. Dowsett (1971) agrees.

As one proceeds south, the situation is complicated by the fact that the forests descend to lower and lower altitudes and finally merge with the lowland forest of the East African Coastal District to form a Southern Temperate Forest (Liversidge 1959*b*; Winterbottom 1968). It is still further complicated by differences in the ecological preferences of species in tropical and temperate areas. The Limpopo and Zambezi valleys must always have isolated these southern montane forests into two blocks, cut off by the Zambezi from the montane areas to the north. Whether one is justified in splitting off the montane and temperate forests south of the Limpopo as a distinct South Temperate Forest District or whether it is better to regard them as a sub-district of the East African Montane District is a moot point, but as they include a number of endemic species, such as *Cossypha dichroa*, *Bradypterus sylvaticus* and *Erythropygia signata*, besides lacking many forms widespread further north (e.g. *Alethe* spp., *Arizelocichla* spp., *Cryptospiza* spp.), they cannot be 'lumped' with the East African Montane forests without some distinction being drawn.

In an endeavour to find out what might have become of our temperate and montane forests in South Africa during the Pleistocene, I first tried to ascertain the factors controlling their natural distribution at present (i.e. ignoring the effects of human interference). Acocks (1953) suggests that the minimum rainfall for forest is 30–35 inches (*c.* 762–889 mm) per annum. But it is clear, from the absence of forest at high altitudes on the Drakensberg and the mountains of the south-west Cape, that some other factor must be involved as well. The most probable of these is temperature.

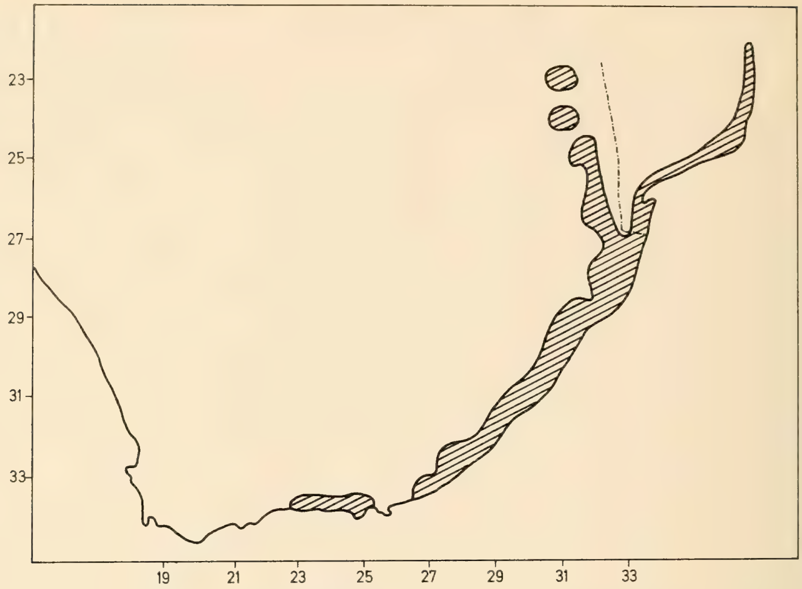
Zeuner (1959) states that the minimum for tree growth is a temperature in excess of 10°C. in summer; but this relates to the northern taiga and not to the temperate broad-leafed forest. In fact, the only place in South Africa where this condition might apply if the temperature fell by 5°C. is Port Nolloth and the rainfall there is inadequate for tree growth anyway.

I therefore plotted the rainfall against the average minimum monthly temperature of the coldest month for those meteorological stations in the vicinity of which forest occurs or was known to occur in the recent past. The bulk of these fell into a zone demarcated by the 850 mm isohyet and the 8°C. isotherm; but in the extreme south, forest could occur with 700 mm of rain and a minimum average temperature of 7°C. in the coldest month. In South America, *Nothofagus* forest occurs at much lower temperatures than this but *Nothofagus* apparently never occurred in Africa.

I then made the assumptions that during a hypothermal period, the temperature would drop 5°C. and the effectiveness of the rainfall would increase by 25%. Cooke (1962) has produced a map showing the hypothetical vegetation with a rainfall of 150% of that at present, but this seemed to me excessive.

The next step was to plot those meteorological stations which met these two requirements—i.e. those with a minimum monthly average temperature of 13°C. or more in the coldest month and a rainfall of at least 640 mm.

The map so obtained (Map 8) suggests that, except close to sea-level, forest could not grow along the south coast except between Knysna and Humansdorp; that there would be a block of forest along the coastal lowland from Alexandria to St. Lucia and thence west of the Lebombo Mountains to about 24°30′S., though the forest may not have been completely continuous. There would be further montane forest blocks in the north-eastern Transvaal, major enlargements of the existing Woodbush and Soutpansberg forests but lower down the mountains, though not descending into the Limpopo valley. It also appears that the Kasane area, at the junction of the Zambezi and Chobe, would have been



Map 8. Suggested forest country during a pluvial period.

able to support forest—there is, of course, riverine ('gallery') forest there today. This forest would not reach as far east as the Victoria Falls; and as its postulated existence depends on the assumption that the increased effectiveness of the rainfall would be the same there as in the south, the suggestion is decidedly speculative.

The big coastal block referred to above is mapped by Cooke (1962) as 'Tropical forest-savanna mosaic' and he extends it up into coastal Mozambique as far as Beira. I did not carry my own investigations into Mozambique but the rainfall map of the South African Weather Bureau supports Cooke's idea that the conditions along the coast there would be much the same as in Natal and Zululand and this has been adopted in my map.

The southern (Knysna) forest block of my map is shown by Cooke as 'Subtropical mixed woodland', which seems to me unlikely.

My map suggests that the temperate (montane) forest and the tropical lowland forest would merge along the Pongola River about latitude 27°S., which is some 4–5° further north than they do today. In East Africa, including Rhodesia, a faunal change in continuous forest cover occurs rather abruptly at an altitude which naturally varies according to the latitude; but this change does not coincide with any change in the botanical nature of the forest. Further south, where lowland and montane forest are separated by drier areas, the avifaunas of the two differ somewhat but chiefly at the subspecific level. Further south still, the two forest types merge into a temperate lowland forest and the avifauna contains elements of both, plus some endemics. It would presumably be forest of this type which extended north to Zululand in the Pleistocene hypothermals and its greater extent and fragmentation during arid periods would give more scope for the development of these endemics.

I have not considered here whether the lowering of the sea level, and the consequent exposure of much of the present Agulhas Bank, would affect the issue. This has been discussed briefly elsewhere (Winterbottom 1968) and my conclusion was that it would be unlikely to be important.

The avifauna of the montane grasslands and heath-*Protea* complex in Rhodesia includes one endemic species, *Prinia robertsi*; a number of species of wider distribution further south but confined to this area in Rhodesia, such as *Sarothrura affinis*, *Sphenoeacus afer*, *Malaconotus zeylonus*, *Promerops gurneyi*, *Nectarinia famosa*, and *Serinus canicollis*; and montane species of East Africa, here at the southern end of their range, like *Apus myoptilus* and *Nectarinia kilimensis*. Of a list of 58 non-forest montane species in Malawi (based on Benson 1953), ten (17%) do not occur south of the Zambezi.

In the montane non-forest areas south of the Limpopo, there are a number of other species restricted to this type of habitat there but occurring down to sea-level further south. Examples are *Geocolaptes olivaceus* and *Serinus tottus*.

Although the montane forests north of the Limpopo are regarded as a distinct district, this is not the case with the lowland forests of East Africa. These differ from the West African lowland forests in their broken and slighter extent, so that many of the species extend out of the forest into dense scrub. I have listed only six species (*Neocossyphus poensis*, *Bias musicus*, *Malacocincla rufipennis*, *Dicrurus ludwigii*, *Nectarinia olivacea* and *Mandingoa nitidula*) which occur in the West African forests and again in the coastal forests of the east but not in between, and two cases in which one member of a superspecies inhabits the West African forests and another the East African (*Macrosphenus concolor* and *M. kretschmeri*; and *Erythrocercus mccalli* and *E. holochlorus*), so that the avifaunas of the two are quite distinct and it is simplest to regard the East African coastal forests as a habitat of the East African Coastal District. This difference between montane and lowland forest becomes intelligible if we realize that when forest was at its maximum, during a pluvial, the lower temperature would favour montane, rather than lowland, forest; that the avifaunas of the two forest types are largely distinct (Moreau (1952) estimates that 90% of the montane forest avifauna is confined to that habitat and does not occur in lowland forest); and that therefore there is unlikely to have been any direct connection between the lowland forest of east and west.

FRESHWATER

As I have shown elsewhere (Winterbottom 1967), the freshwater avifauna of eastern and northern South Africa forms part of the East African tropical aquatic avifauna; but that of the west and south-west is rather different.

The tropical avifauna, which extends south to St. Lucia, has been fully discussed and described elsewhere (Winterbottom 1967, 1972*a*). It comprises 52 species, excluding Palaearctic migrants and species characteristic of reed-beds (e.g. *Acrocephalus* spp.). A further ten species are sufficiently widespread to suggest that they, too, should be included. The fauna, which has already been set out in papers cited above and also in Ruwet (1965), is:

Phalacrocorax lucidus, *P. africanus*, *Anhinga rufa*, *Pelecanus rufescens*, *Nycticorax nycticorax*, *Butorides striatus*, *Ardeola rufiventris*, *A. ralloides*, *A. ibis*, *Egretta ardesiaca*, *E. garzetta*, *E. intermedia*, *E. alba*, *Ardea cinerea*, *A. melanocephala*, *A. goliath*, *A. purpurea*, *Ixobrychus minutus*, *Scopus umbretta*, *Ibis ibis*, *Leptoptilos crumeniferus*, *Ephippiorhynchus senegalensis*, *Anastomus lamelligerus*, *Threskiornis aethiopica*, *Plegadis falcinellus*, *Bostrychia hagedash*, *Platalea alba*, *Thalassornis leuconotus*, *Sarkidiornis melanotos*, *Dendrocygna viduata*, *D. bicolor*, *Nettapus auritus*, *Plectropterus gambensis*, *Anas erythrorhyncha*, *Rallus caerulescens*, *Limnocorax flavirostra*, *Gallinula chloropus*, *Porphyrio porphyrio*, *Balaearica pavonina*, *Actophilornis africanus*, *Vanellus senegallus*, *V. armatus*, *V. crassirostris*, *Himantopus himantopus*, *Gallinago nigripennis*, *Larus cirrocephalus*, *Glareola pratincola*, *Chlidonias leucoptera*, *Alcedo cristata*, *Ceryle rudis*, *C. maxima*.

For southern African areas, we should add *Pelecanus onocrotalus*.

The temperate aquatic avifauna of the south-west, based on species occurring in at least 5% of 1 210 lists, consists of 49 species, as follows:

Podiceps cristatus, *P. nigricollis*, *P. ruficollis*, *Pelecanus onocrotalus*, *Phalacrocorax lucidus*, *P. africanus*, *Anhinga rufa*, *Ardea cinerea*, *A. melanocephaal*, *A. purpurea*, *Egretta garzetta*, *E. intermedia*, *Ardeola ibis*, *Nycticorax nycticorax*, *Scopus umbretta*, *Threskiornis aethiopica*, *Platalea alba*, *Phoenicopterus ruber*, *P. minor*, *Plecotropterus gambensis*, *Alopochen aegyptiacus*, *Tadorna cana*, *Anas smithii*, *A. undulata*. *A. erythrorhyncha*, *A. capensis*, *Netta erythrophthalma*, *Oxyura punctata*, *Haliaeetus vocifer*, *Circus ranivorus*, *Limnocorax flavirostra*, *Porphyrio porhpyrio*, *Gallinula chloropus*, *Fulica cristata*, *Charadrius marginatus*, *C. pecuarius*, *C. tricollaris*, *Vanellus armatus*, *Gallinago nigripennis*, *Recurvirostra avosetta*, *Himantopus himantopus*, *Burhinus vermiculatus*, *Ceryle rudis*, *Alcedo cristata*, *Riparia paludicola*, *Acrocephalus gracilirostris*, *Bradypterus babaecalus*, *Cisticola tinniens* and *Motacilla capensis*.

Non-breeding migrants from the Palaearctic, visitors from the sea-coast (e.g. *Larus novaehollandiae*) and species which forage on the shores but breed elsewhere (e.g. *Macronyx capensis*) are excluded.

Of the above 49 species, only 22 (45%) occur also in the tropical list and the Coefficient of Community is 25; so that the two are very distinct.

I have also suggested that the Karoo-Damaraland water birds may form a distinct assembly. The fauna, based on South West African and Karoo lists, numbers 28 species, namely:

Podiceps ruficollis, *Phalacrocorax lucidus*, *P. africanus*, *Ardea cinerea*, *A. melanocephala*, *Scopus umbretta*, *Ciconia nigra*, *Ibis ibis*, *Platalea alba*, *Alopochen aegyptiacus*, *Tadorna cana*, *Anas smithii*, *A. undulata*, *A. sparsa*, *A. capensis*, *A. erythrorhyncha*, *Oxyura punctata*, *Gallinula chloropus*, *Fulica cristata*, *Charadrius pecuarius*, *C. tricollaris*, *Vanellus armatus*, *Recurvirostra avosetta*, *Himantopus himantopus*, *Larus cirrocephalus*, *Acrocephalus baeticatus*, *Cisticola tinniens* and *Motacilla capensis*.

The Coefficient of Community between this fauna and that of the south-west is only 43; but Simpson's Coefficient:

$$\frac{c}{n_1} \times 100$$

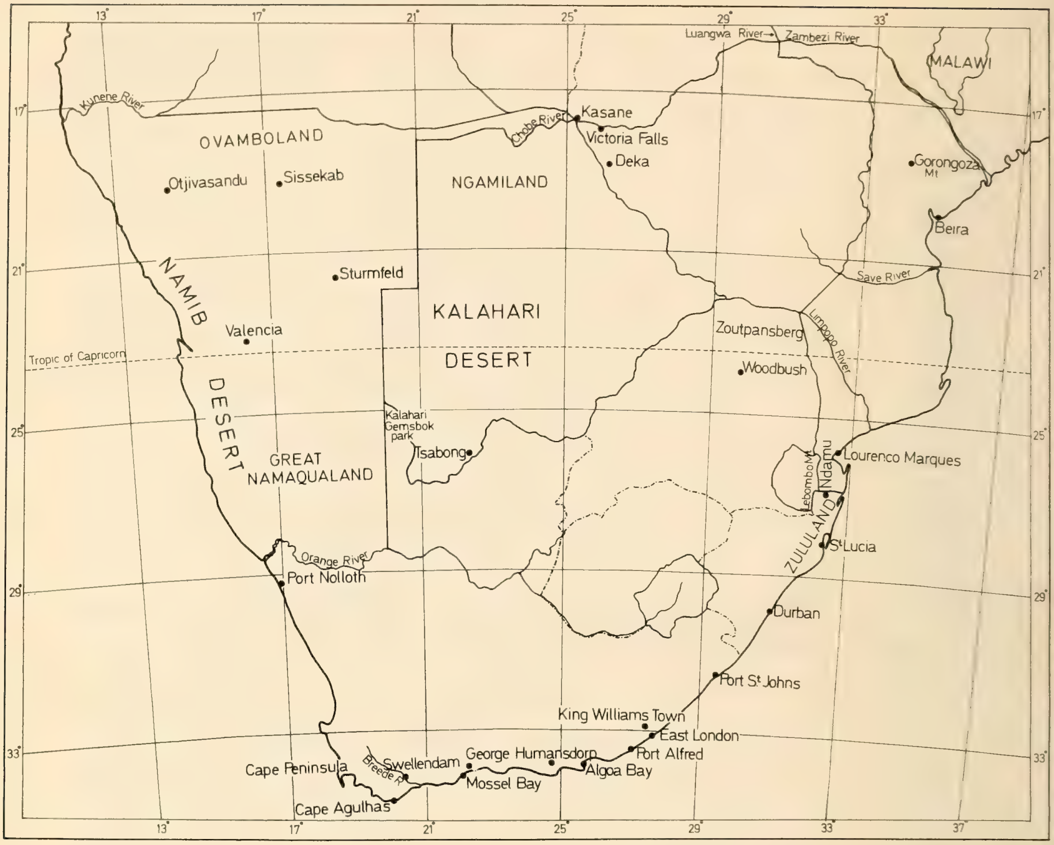
where c is the number of species in common and n_1 is the number in the smaller fauna, is 82, suggesting that this fauna may be little more than an impoverished version of that of the south-west. It should be noted, however, that *Anas undulata*, despite the map in McLachlan & Liversidge (1970), and *Cisticola tinniens* occur only in the south and not in South West Africa and the validity of their inclusion is thus rather doubtful. Their exclusion would reduce Simpson's Coefficient to 75. With the tropical fauna, Simpson's Coefficient is only 43. The distribution pattern of most aquatic birds in South West Africa is a narrow strip down the centre, between the Namib and the Kalahari, and only extending as far south as about 25°S., though some of this may be due to lack of observations at the time water is present in the south. On the whole, I think it would be better to keep this fauna distinct as a South West Arid aquatic avifauna.

COASTAL

The birds of the South African coasts show an east–west difference in their distribution, very largely correlated with the cold current on the west coast and the warm one on the east. The rich avifauna of the west coast is characterized by the presence as breeding species of *Spheniscus demersus*, *Sula bassana*, *Phalacrocorax lucidus*, *P. capensis*, *P. neglectus*, *P. africanus coronatus*, *Haematopus moquini*, *Charadrius marginatus*, *Larus novaehollandiae*, *L. dominicanus*, *Sterna bergii* and *S. balaenarum*. The section from Cape L'Agulhas to Algoa Bay may be regarded as a transition zone, east and north of which the coastal fauna is an impoverished one, with, from Zululand north, a small tropical component *Dromas ardeola*, *Sterna fuscata* and *S. benghalensis* being the most important; but none of these breeds within our limits. The only coastal-breeding species given by Clancey (1971) for southern Mozambique are *Charadrius marginatus*, *Sterna bergii* and *Hydroprogne caspia*.

OCEANIC

As Liversidge (1959*a*) has pointed out, oceanic waters in South Africa belong to the Southern Oceans of Alexander (1955). The Southern Oceans are characterized by the wealth of Sphenisciformes and Procellariiformes, plus a few species of other groups, such as *Sterna vittata*. The only uncertain point is just where this Southern Oceans avifauna gives place to that of the Tropical Oceans. Serventy, Serventy & Warham (1972) have placed the limit of the



Map 9. Places mentioned in the text.

Sub-Antarctic avifauna at the Sub-tropical Convergence; but have, in effect, admitted the invalidity of this by extending the boundary northwards to include the southern coasts of Australia. The idea that the Sub-tropical Convergence constitutes a faunal boundary for birds no doubt stems from Murphy (1936), who considered that 'the majority of oceanic birds are bound as peons to their own specific types of surface water'. This is an exaggeration (Winterbottom 1971*b*). In the Atlantic, the boundary between the Southern Oceans and the Tropical Seas appears to be about the Tropic of Capricorn; on the east coast, it may be about the same latitude—of the 13 species recorded by Rand (1962) in a transect along 28°S., all but *Sterna fuscata* were birds of the Southern Oceans fauna; but the breeding sea birds of Europa Island, in about 22°S., are tropical—*Sula sula*, *Fregata minor*, *Phaethon* spp. and *Sterna fuscata* (Malzy 1966). The distribution of marine birds in the Indian Ocean is poorly known (Watson, Zusi & Storer 1963) but of the 18 tropical species, ten have been recorded within South African limits, mostly as stragglers.

Of the predominantly marine families, the Spheniscidae, Diomedeidae, Procellariidae, Hydrobatidae, Sulidae, Phalacrocoracidae, Stercorariidae and Laridae, South African seas are inhabited by 54 species, excluding such freshwater forms as *Larus cirrocephalus* and *Chlidonias* spp. in the Laridae and the tropical terns, boobies, tropic-birds and frigate-birds which reach the area only marginally. Of these, 11 species breed (and are more typical of the coasts than the ocean) and another 11 are migrants from the north. The remaining 32 species all breed in the south, ten of them (plus *Larus dominicanus*, which also breeds in South Africa) south of 60°S. Attempts to divide the avifauna of the south into Antarctic and Sub-Antarctic have been made by Murphy (1964) and Voous (1965) but there are only three marine birds whose breeding is wholly confined to the Antarctic (*Thalassoica antarctica*, *Fulmarus glacialoides* and *Pagodroma nivea*) and the first two of these range far to the north out of the breeding season. It may therefore be doubted if it is really profitable to make such a distinction. As I have pointed out elsewhere (Winterbottom 1971*b*), the influence of surface waters has been over-emphasized (except possibly in the case of penguins, whose distribution when not breeding is very poorly known) and I agree with Alexander in including all waters south of the Tropical Convergence in a single zoogeographical district, the Southern Oceans. To this district, South African offshore waters belong. It should be noted, however, that not a single species of the Procellariiformes breeds in South African waters.

SUMMARY

South Africa forms part of the Ethiopian Zoogeographical Region. Its birds exhibit five distinct patterns of geographical distribution: oceanic birds, coastal birds, freshwater birds, forest birds and the rest.

Almost the whole of oceanic waters off the South African coast are inhabited by birds of the Southern Oceans Zoogeographical Region.

Coastal birds show a difference between east and west correlated with the warm and cold currents; the eastern avifauna is impoverished and, in the north, has a small tropical element.

Freshwater birds fall into three groups, an eastern tropical, a southern temperate and a western.

The avifauna of the mountain forests of Rhodesia and Mozambique forms a sub-district of the East African Montane District of Chapin (1932). The avifauna of the temperate forests south of the Limpopo is rather more distinct; but the tropical forests of the lowlands of Mozambique and Zululand are best regarded as a habitat of the East African Coastal District.

For the remaining land birds, the pattern suggested by their distribution comprises four districts, three of which extend beyond the borders of South Africa, and a transitional zone. Sub-districts are recognizable for three of these districts.

The districts and sub-districts are:

- South Central Highlands District
- South West Arid District
    - Damaraland Sub-district
    - Kalahari Sandveld Sub-district
    - Kalahari Thornveld Sub-district
- East African Coastal District
    - Mozambique Sub-district
    - Southern Sub-district
- South Temperate District
    - Karoo Sub-district
    - Highveld Sub-district
    - Winter Rainfall Sub-district

The transition zone lies between the South Central Highlands and the South West Arid Districts.

ACKNOWLEDGEMENTS

In matters of past plant distribution, I have had the advantage of conversations with Professor E. M. van Zinderen Bakker and Professor E. Schelpe, who must not, however, be held responsible for the views expressed here. I have also had discussions and correspondence on zoogeography with Dr J. C. Poynton, whose views I have found stimulating—especially when I disagreed with them! My colleagues, Professor W. R. Siegfried and Mrs M. K. Rowan, read the whole MS and made helpful suggestions.

For anything concerning the distribution of passerine birds I have found Hall & Moreau (1970) invaluable—without it, this paper would have contained many more inaccuracies than no doubt it does. For non-passerines, I have used White (1965), also a useful work of reference. For the detailed distribution of birds within South Africa, I have used the various numbers of the *South African Avifauna Series*, published by the Percy FitzPatrick Institute of African Ornithology, and the numerous MS lists filed in the Institute, especially my own and those of C. J. Skead, whose meticulous work on the birds of the eastern Cape Province has been invaluable.

The section on the western districts incorporates most of a paper presented at the XV Congressus Internationalis Ornithologicus, where my views on the desirability of two districts in this area were first put forward (Winterbottom 1970).

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APPENDIX

English names of birds mentioned in the text

Achaetops pycnopygius—Damara Rockjumper
Acrocephalus baeticatus—South African Marsh-Warbler
gracilirostris—Cape Reed-Warbler
Actophilornis africanus—African Jaçana
Agapornis roseicollis—Rosy-faced Lovebird
Agalaius phoeniceus—Red-winged Blackbird
Alaemon burra—Red Lark
grayi—Gray's Lark
Alcedo cristata—Malachite Kingfisher
Alopochen aegyptiacus—Egyptian Goose
Amadina erythrocephala—Red-headed Finch
fasciata—Cut-throat Finch
Anas capensis—Cape Teal
erythrorhyncha—Red-billed Teal
smithii—Cape Shoveller
sparsa—Black Duck
undulata—Yellow-billed Duck
Anastomus lamelligerus—Openbill
Andropadus flaviventris—Yellow-breasted Bulbul
importunus—Sombre Bulbul
virens—Little Greenbul
Anhinga rufa—African Darter
Anthoscopus minutus—Penduline Tit
Anthreptes neglecta—Ulunguru Violet-backed Sunbird
reichenowi—Blue-throated Sunbird
Anthropoides paradisea—Blue Crane
Anthus chloris—Yellow-breasted Pipit
crenatus—African Rock-Pipit
melindae—Malindi Pipit
sokokensis—Sokoke Pipit
Apalis ruddi—Rudd's Apalis
Apus myoptilus—Scarce Swift
Ardea cinerea—Grey Heron
goliath—Goliath-Heron
melanocephala—Black-headed Heron
purpurea—Purple Heron
Ardeola ibis—Cattle-Egret
ralloides—Squacco Heron
rufiventris—Rufous-bellied Heron
Balaearica pavonina—Crowned Crane
Batis fratrum—Woodwards' Batis
pririt—Pririt Batis
Bias musicus—Black-and-White Flycatcher
Bostrychia hagedash—Hadeda
Bradypterus babaecalus—African Sedge-Warbler
barratti—Scrub-Warbler
sylvaticus—Knysna Scrub-Warbler
victorini—Victorin's Warbler
Bubalornis albirostris—Buffalo-Weaver
Bubo capensis—Cape Eagle-Owl
Burhinus vermiculatus—Water-Dikkop
Butorides striatus—Green-backed Heron
Calandrella conirostris—Pink-billed Lark
fringillaris—Botha's Lark
sclateri—Sclater's Lark

Calandrella starki—Stark's Lark
Calendula magnirostris—Thick-billed Lark
Camaroptera stierlingi—Stierling's Barred Warbler
subcinnamomea—Cinnamon-breasted Warbler
Campethera abingoni—Golden-tailed Woodpecker
bennetti—Bennett's Woodpecker
notata—Knysna Woodpecker
Centropus cupreicaudus—Coppery-tailed Coucal
Cercomela schlegelii—Karoo Chat
sinuata—Sickle-winged Chat
tractrac—Tractrac Chat
Certhilauda albescens—Karoo Lark
albofasciata—Spike-heeled Lark
curvirostris—Long-billed Lark
Ceryle maxima—Giant-Kingfisher
rudis—Pied Kingfisher
Ceuthmochares aereus—Green Coucal
Charadrius marginatus—White-fronted Plover
pecuarius—Kittlitz's Plover
tricollaris—Three-Banded Plover
Chlidonias leucoptera—White-winged Black Tern
Ciconia ciconia—White Stork
nigra—Black Stork
Circus maurus—Black Harrier
ranivorus—African Marsh-Harrier
Cisticola dambo—Black-tailed Cisticola
juncidis—Fan-tailed Cisticola
pipiens—Chirping Cisticola
subruficapilla—Grey-backed Cisticola
tinniens—Le Vaillant's Cisticola
Colius colius—White-backed Mousebird
Coracias spatulata—Racket-tailed Roller
Cossypha dichroa—Chorister-Robin
heuglini—Heuglin's Robin
Cursoirus rufus—Burchell's Courser
Dendrocygna bicolor—Fulvous Tree-Duck
viduata—White-faced Duck
Dicrurus adsimilis—Fork-tailed Drongo
ludwigii—Square-tailed Drongo
Dromas ardeola—Crab-Plover
Egretta alba—Great White Egret
ardesiaca—Black Heron
garzetta—Little Egret
intermedia—Yellow-billed Egret
Emberiza capensis—Cape Bunting
impetuani—Lark-like Bunting
Ephippiorhynchus senegalensis—Saddle-billed Stork
Eremomela gregalis—Karoo Green Warbler
Eremopterix australis—Black-eared Finch-Lark
verticalis—Grey-backed Finch-Lark
Erythrocercus holochlorus—Little Yellow Flycatcher
livingstonei—Livingstone's Flycatcher
mccalli—Chestnut-capped Flycatcher
Erythropygia coryphaeus—Karoo Robin
paena—Kalahari Robin
quadrivirgata—Bearded Robin
signata—Brown Robin
Estrilda erythronotos—Black-cheeked Waxbill
Euplectes axillaris—Red-shouldered Widowbird

Euplectes nigroventris—Zanzibar Red Bishop
Eupodotis afer—Black Korhaan
caerulescens—Blue Korhaan
ruficrista—Red-crested Korhaan
vigorsii—Karoo Korhaan
Eurystomus glaucurus—Broad-billed Roller
Francolinus adspersus—Red-billed Francolin
africanus—Grey-winged Francolin
capensis—Cape Francolin
hartlaubi—Hartlaub's Francolin
levaillantoides—Orange River Francolin
rovumae—Rovuma Francolin
sephaena—Crested Francolin
Fregata minor—Greater Frigatebird
Fulica cristata—Red-knobbed Coot
Fulmarus glacialoides—Antarctic Fulmar
Gallinago nigripennis—Ethiopian Snipe
Gallinula chloropus—Moorhen
Geocolaptes olivaceus—Ground-Woodpecker
Geronticus calvus—Bald Ibis
Glareola pratincola—Pratincole
Gutter edouardi—Crested Guineafowl
Haematopus moquini—Black Oystercatcher
Halcyon senegaloides—Mangrove-Kingfisher
Haliaeetus vocifer—Fish-Eagle
Himantopus himantopus—Black-winged Stilt
Hirundo albigularis—White-throated Swallow
spilodera—Cliff-Swallow
Hydroprogne caspia—Caspian Tern
Hypargos niveoguttatus—Red-throated Twinspot
Ibis ibis—Wood-Ibis
Ixobrychus minutus—Little Bittern
Lagonosticta senegala—Red-billed Firefinch
Lamprotornis acuticaudus—Sharp-tailed Starling
australis—Burchell's Starling
corruscus—Black-bellied Starling
mevesii—Long-tailed Starling
nitens—Cape Starling
Laniarius aethiopicus—Tropical Boubou
atrococcineus—Crimson-breasted Shrike
bicolor—Western Boubou
Lanioturdus torquatus—White-tailed Shrike
Lanius collaris—Fiscal-Shrike
souzae—Souza's Shrike
Larus cirrocephalus—Grey-headed Gull
dominicanus—Southern Black-backed Gull
novaehollandiae—Hartlaub's Gull
Leptoptilus crumeniferus—Marabou
Limnocorax flavirostra—Black Crake
Lioptilus nigricapillus—Bush-Blackcap
Macrodipteryx vexillarius—Pennant-winged Nightjar
Macronyx aurantigula—Pangani Longclaw
capensis—Orange-throated Longclaw
croceus—Yellow-throated Longclaw
Macrosphenus concolor—Grey Longbill
kretschmeri—Kretschmer's Longbill
Malacocincla rufipennis—Pale-breasted Illadopsis
Malaconotus quadricolor—Gorgeous Bush-Shrike
zeylonus—*Bokmakierie*

Mandingoa nitidula—Green Twinspot
Melaenornis infuscatus—Chat-Flycatcher
  mariquensis—Marico Flycatcher
  silens—Fiscal-Flycatcher
Melierax canorus—Chanting Goshawk
  metabates—Dark Chanting Goshawk
Merops apiaster—European Bee-eater
  pusillus—Little Bee-eater
Mirafra africanoides—Fawn-coloured Lark
  apiata—Clapper-Lark
  chuana—Short-clawed Lark
  ruddi—Rudd's Lark
  rufocinnamomea—Flappet-Lark
  sabota—Sabota Lark
Monticola angolensis—Angola Thrush
  brevipes—Short-toed Rock-Thrush
  explorator—Sentinel Rock-Thrush
  rupestris—Cape Rock-Thrush
Motacilla capensis—Cape Wagtail
Myioparus boehmi—Böhm's Flycatcher
Myrmecocichla formicivora—Ant-eating Chat
Namibornis herero—Herero Chat
Nectarinia bifasciata—Purple-banded Sunbird
  famosa—Malachite Sunbird
  fusca—Dusky Sunbird
  kilimensis—Bronze Sunbird
  mariquensis—Marico Sunbird
  neergaardi—Neergaard's Sunbird
  olivacea—Olive Sunbird
  pembae—Pemba Sunbird
  senegalensis—Scarlet-chested Sunbird
  veroxii—Grey Sunbird
  violacea—Orange-breasted Sunbird
Neocossyphus poensis—White-tailed Ant-Thrush
Netta erythrophthalma—Southern Pochard
Nettapus auritus—Pygmy-Goose
Nicator gularis—Yellow-spotted Nicator
Nycticorax nycticorax—Night-Heron
Oenanthe monticola—Mountain-Chat
Onychognathus nabouroup—Pale-winged Starling
Ortygospiza locustella—Locust-Finch
Otis kori—Kori Bustard
  ludwigii—Ludwig's Bustard
Oxyura punctata—Maccoa Duck
Pagodroma nivea—Snow-Petrel
Parisoma layardi—Layard's Tit-babbler
  subcaeruleum—Tit-babbler
Parus rufiventris—Rufous Tit
Passer motitensis—Great Sparrow
Pelecanus onocrotalus—White Pelican
  rufescens—Pink-backed Pelican
Phalacrocorax africanus—Reed-Cormorant
  capensis—Cape Cormorant
  lucidus—White-breasted Cormorant
  neglectus—Bank-Cormorant
Phoenicopterus minor—Lesser Flamingo
  ruber—Greater Flamingo
Phyllastrephus debilis—Slender Bulbul
Pinarornis plumosus—Boulder-Chat

Platalea alba—African Spoonbill
Platysteira peltata—Black-throated Wattle-eye
Plectropterus gambensis—Spur-winged Goose
Plegadis falcinellus—Glossy Ibis
Ploceus capensis—Cape Weaver
golandi—Clarke's Weaver
olivaceiceps—Olive-headed Weaver
rubiginosus—Chestnut-Weaver
subaureus—Yellow Weaver
velatus—Masked Weaver
Podiceps cristatus—Great Crested Grebe
nigricollis—Black-necked Grebe
ruficollis—Dabchick
Pogonocichla swynnertoni—Swynnerton's Robin
Pogoniulus bilineatus—Golden-rumped Tinker-Barbet
pusillus—Red-fronted Tinker-Barbet
simplex—Green Tinker-Barbet
Poicephalus cryptoxanthus—Brown-headed Parrot
robustus—Cape Parrot
rueppellii—Rüppell's Parrot
Poliohierax semitorquatus—Pygmy-Falcon
Porphyrio porphyrio—Purple Gallinule
Prinia flavicans—Black-chested Prinia
maculosa—Karoo Prinia
pectoralis—Rufous-eared Prinia
robertsi—Roberts's Prinia
subflava—Tawny-flanked Prinia
substriata—Namaqua Prinia
Prionops scopifrons—Chestnut-fronted Helmet-Shrike
Promerops cafer—Cape Sugarbird
gurneyi—Gurney's Sugarbird
Pterocles burchelli—Spotted Sandgrouse
gutturalis—Yellow-throated Sandgrouse
namaqua—Namaqua Sandgrouse
Pycnonotus barbatus—Black-eyed Bulbul
capensis—Cape Bulbul
nigricans—Red-eyed Bulbul
Rallus caerulescens—Cape Rail
Recurvirostra avosetta—Avocet
Riparia paludicola—African Sand-Martin
Sarkidiornis melanotus—Knob-billed Duck
Sarothrura affinis—Striped Flufftail
Scopus umbretta—Hamerkop
Seicercus laurae—Mrs Boulton's Warbler
Serinus alario—Black-headed Canary
albogularis—White-throated Seed-eater
citrinipectus—Lemon-breasted Canary
flaviventris—Yellow Canary
leucopterus—Protea Seed-eater
mennelli—Black-eared Seed-eater
scotops—Forest-Canary
tottus—Mountain-Siskin
Sheppardia gunningi—Gunning's Robin
Smithornis capensis—African Broadbill
Spheniscus demersus—Jackass-Penguin
Sphenoeacus afer—Grassbird
Sporopipes squamifrons—Scaly Weaver
Spreo bicolor—Pied Starling
fischeri—Fischer's Starling

Stactolaema leucotis—White-eared Barbet
whytii—Whyte's Barbet
Stenostira scita—Fairy-Flycatcher
Sterna balaenarum—Damara Tern
benghalensis—Lesser Crested Tern
bergii—Swift Tern
fuscata—Sooty Tern
vittata—Antarctic Tern
Streptopelia capicola—Cape Turtle-Dove
semitorquata—Red-eyed Dove
senegalensis—Laughing Dove
Sturnella magna—Meadowlark
Sula bassana—Cape Gannet
sula—Red-footed Booby
Sylvietta rufescens—Long-billed Crombec
Tadorna cana—South African Shelduck
Tauraco fischeri—Fischer's Turaco
porphyriolophus—Purple-crested Lourie
Tchagra tchagra—Tchagra
Thalassoica antarctica—Antarctic Petrel
Thalassornis leuconotus—White-backed Duck
Thamnolaea arnoti—Arnot's Chat
Threskiornis aethiopica—Sacred Ibis
Tockus alboterminatus—Crowned Hornbill
bradfieldi—Bradfield's Hornbill
monteiri—Monteiro's Hornbill
Turdoides bicolor—Pied Babbler
gymnogenys—Bare-cheeked Babbler
jardineii—Arrow-marked Babbler
melanops—Black-faced Babbler
squamulatus—Scaly Babbler
Turdus fischeri—Natal Thrush
Uraeginthus granatinus—Violet-eared Waxbill
Vanellus armatus—Blacksmith-Plover
crassirostris—White-winged Plover
senegallus—Wattled Plover
Vidua regia—Shaft-tailed Whydah
Zosterops senegalensis—Yellow White-eye

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960. *Style manual for biological journals.* Washington: American Institute of Biological Sciences.

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

ZOOLOGICAL NOMENCLATURE

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Example

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Volume 66 Band
November 1974 November
Part 7 Deel

PEDI SKIN DRESSING TECHNIQUE

By

E. M. SHAW
&
H. E. BÖHME

Cape Town Kaapstad

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6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R4,40

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ISBN 0 949940 58 5

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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E. M. SHAW & H. E. BÖHME

Photographs by J. B. KRAMER

South African Museum, Cape Town

(With 28 figures)

[*MS accepted 16 November 1973*]

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INTRODUCTION

In May 1973 a visit was made to the BaPedi of the Nebo area of Sekhukhuniland in Lebowa, and at Chief Sekwati's village a demonstration was seen of the process of dressing an ox-skin. The following information about the technique was obtained from Johannes Mogeng Kgolone, who had learnt the craft from his father, and who practised as a specialist skinworker. He had regular assistance from a brother, and called in friends to help with the more strenuous processes involved. On the occasion that we were present at his homestead he rewarded them with beer, and when we gave a few individual presents to those participating he firmly insisted on them all being handed over, which they were without demur.

DESCRIPTION

After the skin is removed from the animal, it is pegged out to dry. It then becomes hard and may be stored like this until needed. To begin the dressing process the skin is soaked in clear water in a three-legged pot (Fig. 1). A stone is placed on the skin to keep it submerged. The moisture softens the skin and the hairs can be removed more easily. When the skin is very well soaked the process of scraping and further softening commences. This is a long procedure which, according to the skinworker, can take from a day, when he has many helpers, to four days. There is a more or less set sequence of events.

The damp skin is held outstretched by four or five men with the hairy side facing upwards and one man proceeds to scrape the skin (removing the hair) with an iron rod, bent in the shape of a U (Fig. 2). This is done till the surface moisture and most of the loose hair is scraped off. The hairy side now has a 'patchy' look (Fig. 3).

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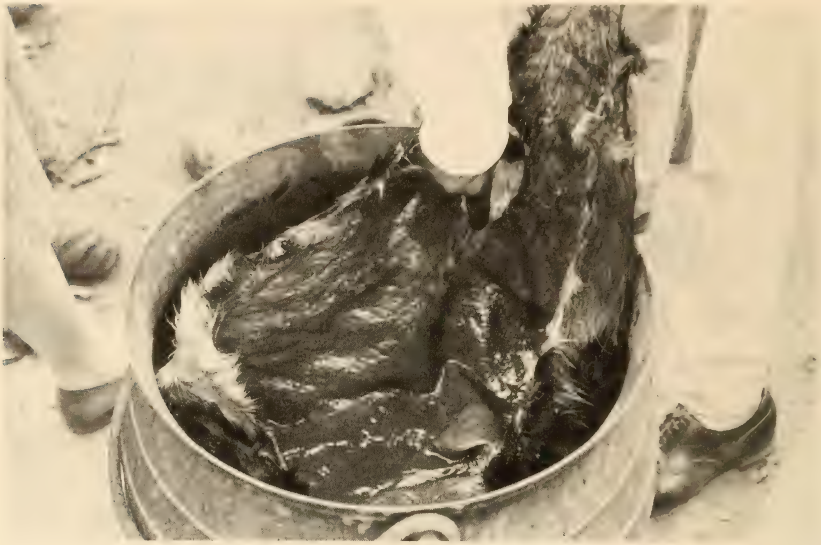

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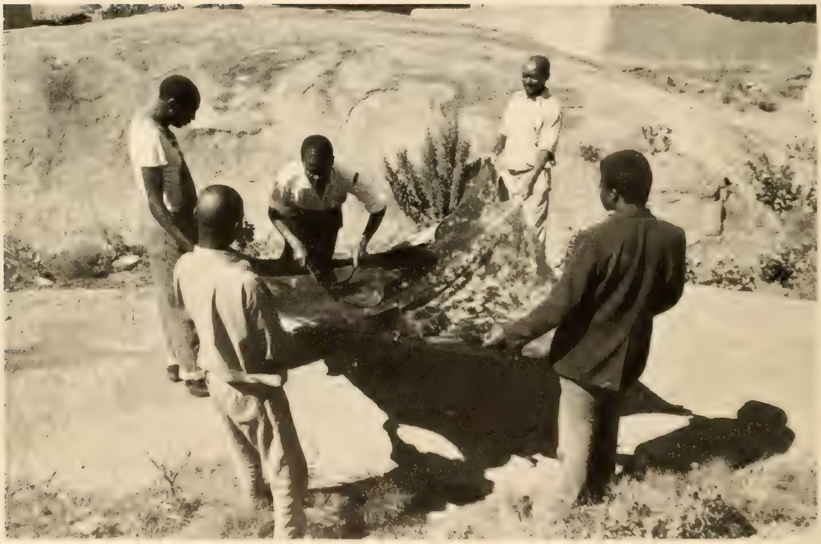

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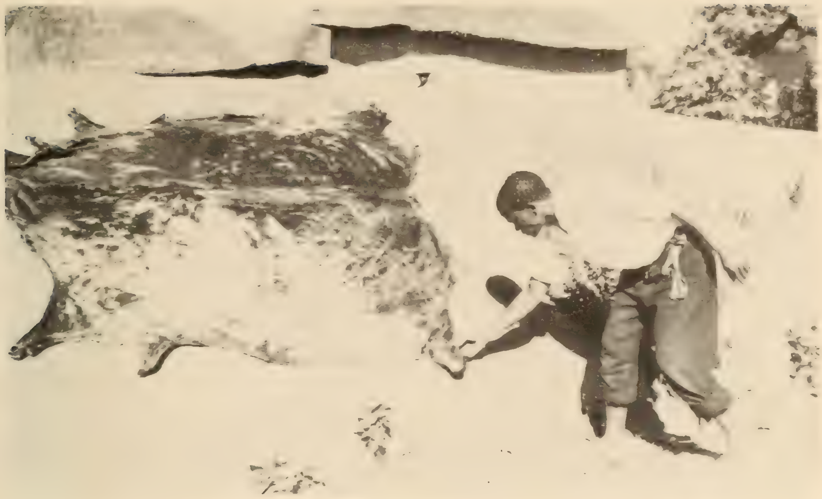
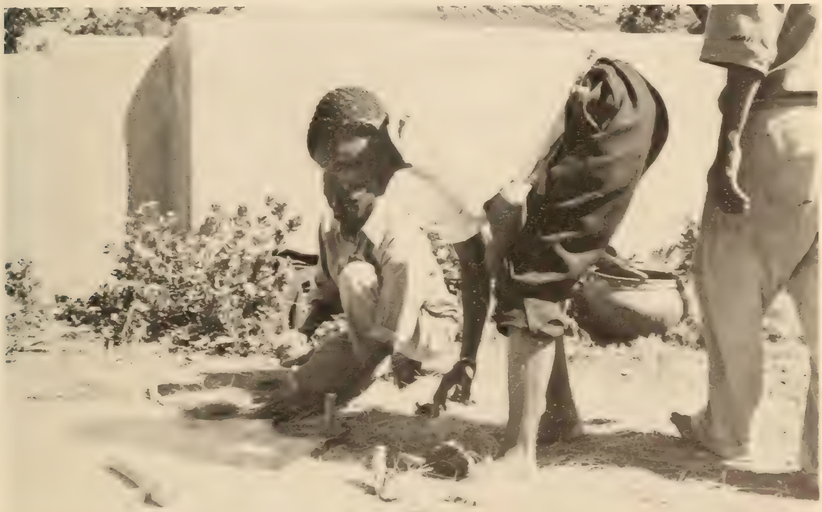


Figure 3

Then the scraped skin is turned over, so that the inner side faces upwards and the hair side down, and is stretched and pegged with wooden pegs on to the ground on a layer of dried grass. The grass is there to keep the wet skin clean. A sack of dried grass is specially kept for this purpose. A stone is used to hit the pegs into the ground (Fig. 4). Various tools are used for scraping and currying but in no definite sequence.



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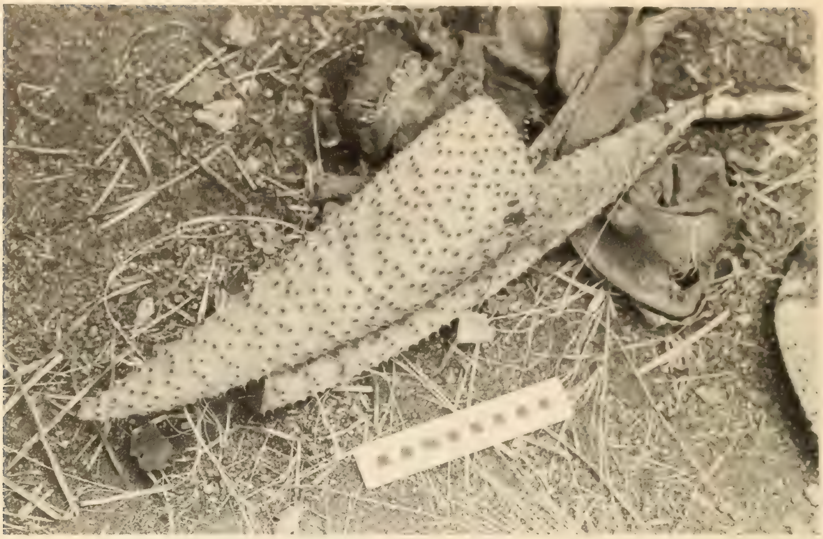
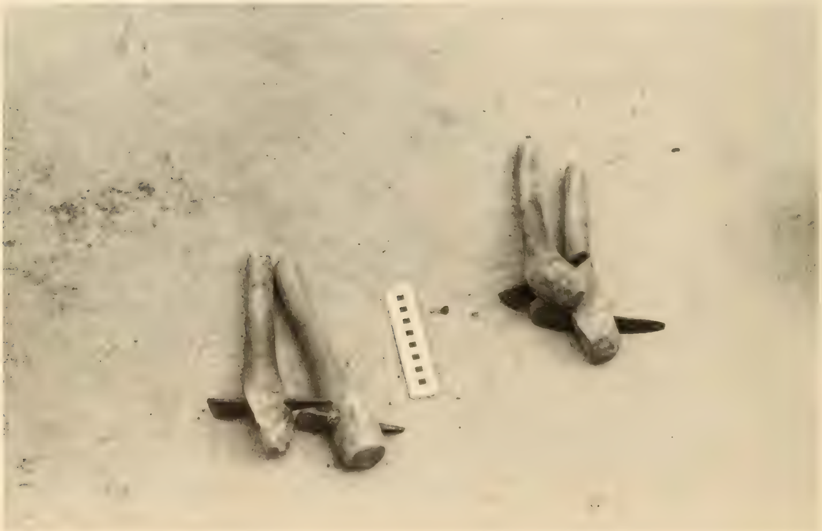


Figure 5

A thorny aloe leaf (*lilabo*) (Fig. 5) and an adze (*lepalo*) (Fig. 6) are used at this stage to scrape the skin. When using the adze each worker first wets his working area and then proceeds to scrape in the following way: the haft of the adze is held in the left hand, while the right hand cups the hafthead and the adze is worked towards him in short jerky movements (Fig. 7).



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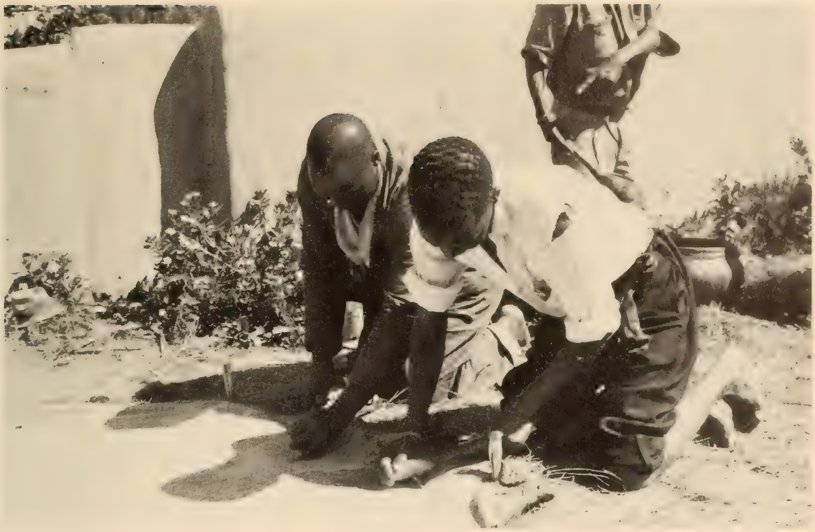
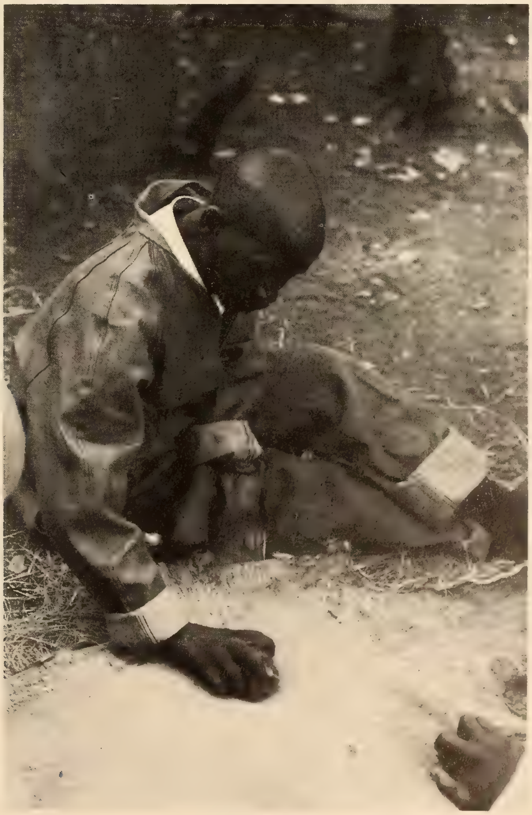


Figure 7

After short intervals of scraping, the blade of the adze is sharpened on an ordinary knife, a whetstone (*selotsu*) or another adze blade.



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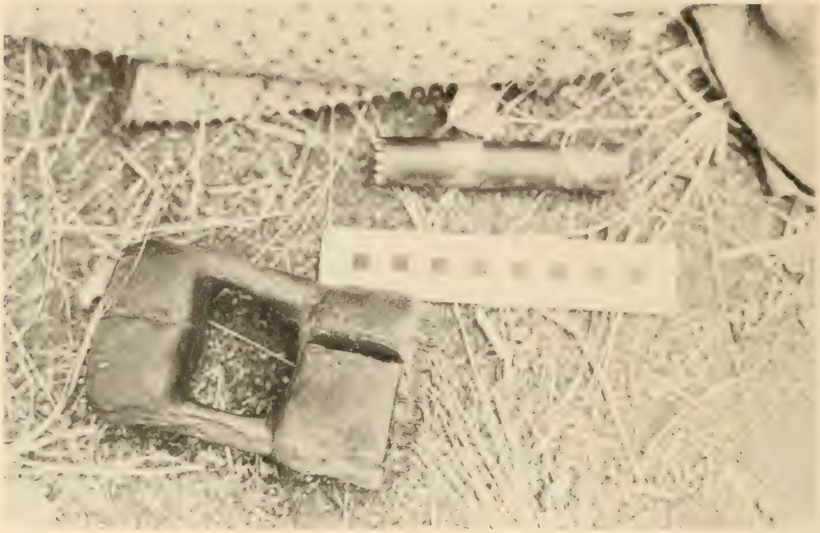
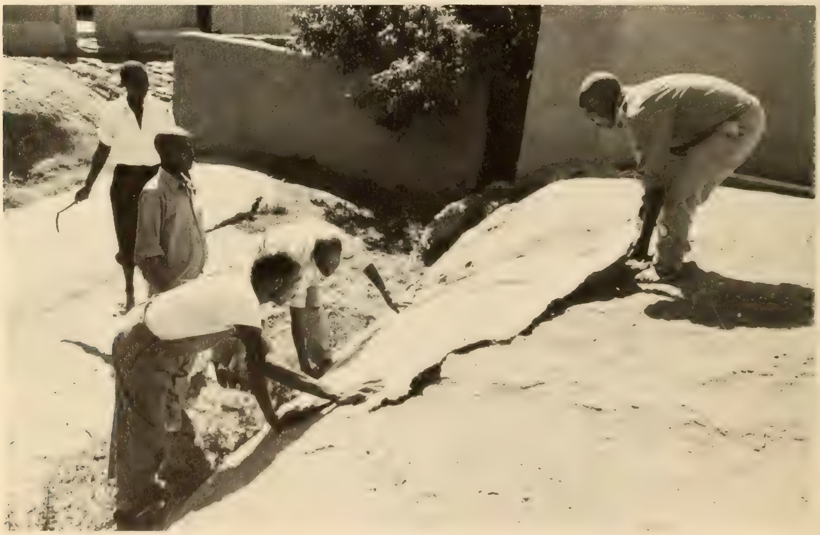


Figure 9

Following the scraping the preparation continues using either rough stones (those seen were pieces of lateritic ironstone) (Fig. 8), *tsela*, a name also given to a wooden handle with rows of metal spikes along its base, or to a hollow metal tube with a serrated edge, or aloe leaves (Fig. 9). Abrading the skin proceeded on this occasion for more than fifteen minutes but would take much longer had the skinworker not had as much help as he had during our stay.



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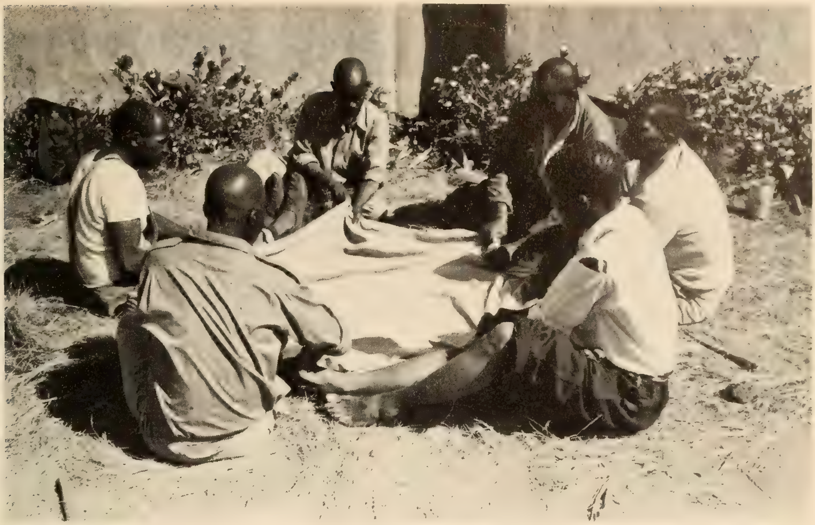
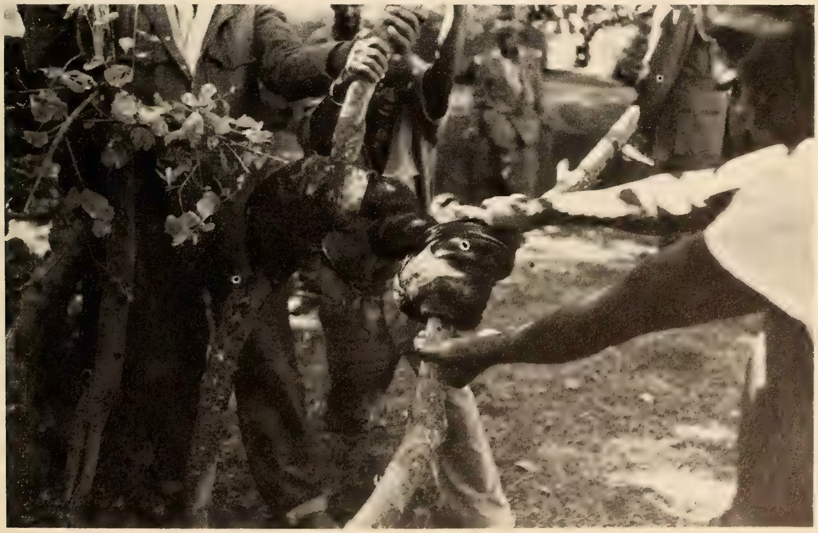


Figure 11

The skin is unpegged and the metal scraper used again to remove any loose scrapings. It is then carried to a near-by boulder where it is left to dry out for a short while in the sun (Fig. 10).

The skin is then softened by rubbing it between the hands (Fig. 11). The next step is to twist it around a tree trunk with a stick (Fig. 12) in order to wring out all the remaining water.



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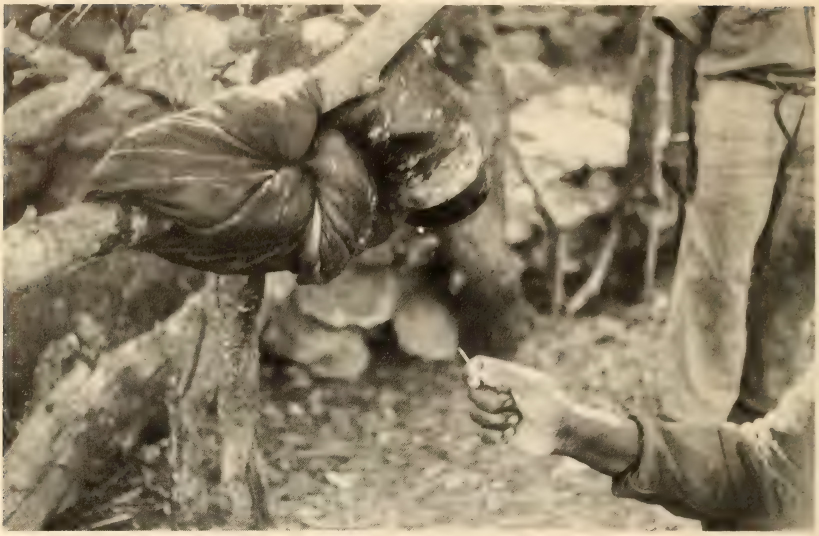
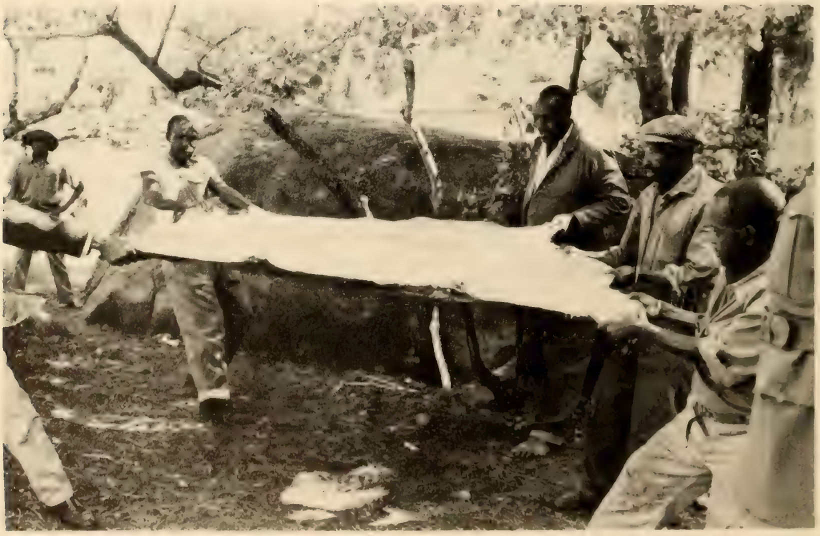


Figure 13

The twisted skin is pricked with a nail to allow all the water to seep out (Fig. 13) and is then opened out and pulled hard to stretch it (Fig. 14). Then follows a long session of braying with the hands. The left hand clasps the skin tightly whereas the right grips it and rolls it over the fist of the left hand. This is repeated over and over, moving from one part of the skin to the next (Fig. 15).



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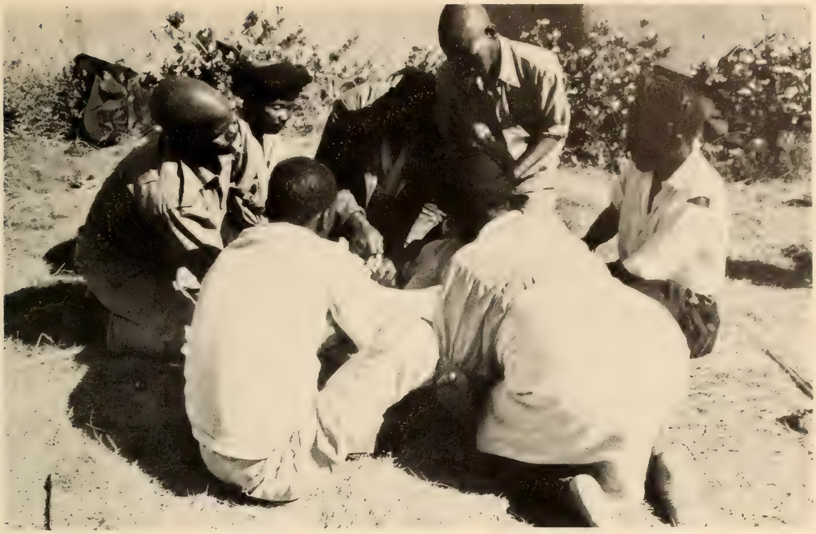
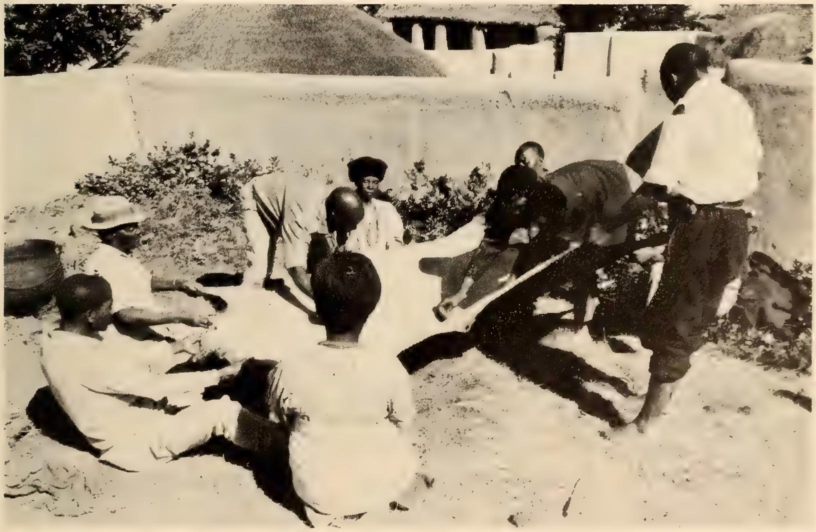


Figure 15

After the skin as been sufficiently softened it is held stretched out again and two helpers scour it with aloe leaves or with *tsela*. One scoured in a diagonal direction whereas the other scraped in parallel movements (Fig. 16). It is then thrown on to the boulder again, this time with the inner side facing the rock.



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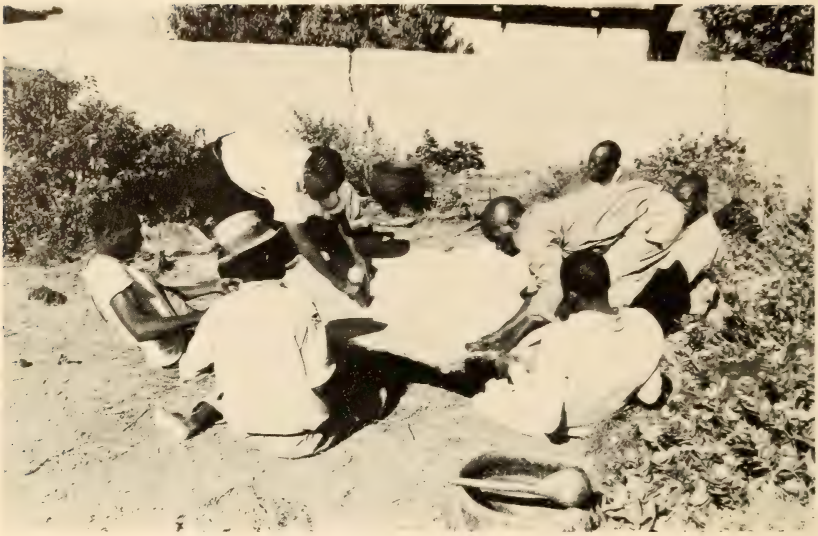
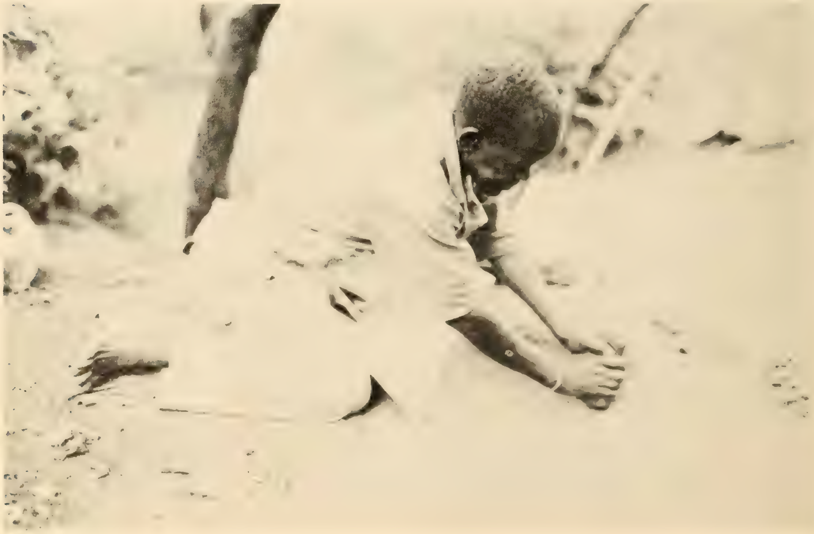


Figure 17

After drying for a while, the skin is kneaded again with the hands. Finally it is pulled taut and the aloe leaf or the *tsela* rubbed over it to raise a pile (Fig. 17). At this stage the skin is still quite damp.



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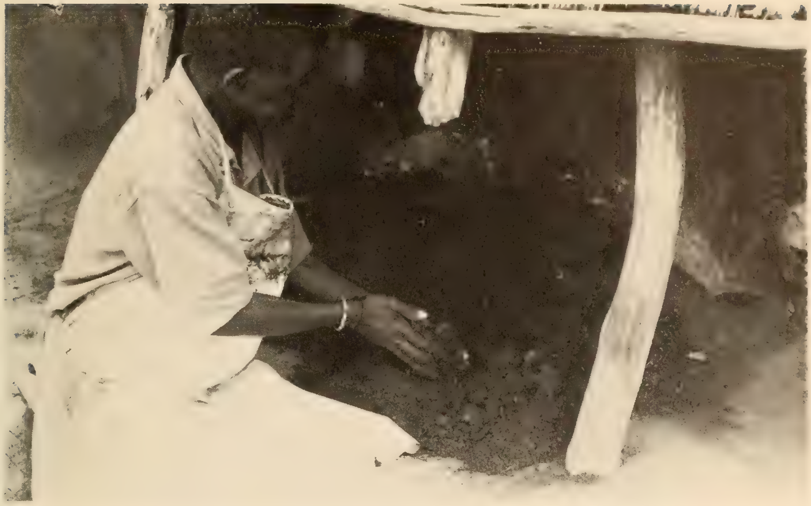


Figure 19

The next step is to smear the skin with fat from the fruit (*ditshidi*) of the *mochidi* tree (*Ximenia caffra* Sond.). The small fruit is red when ripe but turns black on boiling. After boiling it is allowed to dry out and then the kernel is taken out and ground between grinding stones till it forms an oily paste (Fig. 18). The skin is again pegged out, hair-side down on the layer of dried grass and the fat is rubbed into the inner side of the skin with a wooden peg (*pabolo*).

After some time the hide is again brayed, rubbed and wrung with the hands to help the fat to draw deep into the skin.

The hide is now ready to be cut but before doing this the skinworker uses an ordinary knife to straighten it out. Then he proceeds to cut a garment to the required shape. The article seen was a woman's back apron or skirt, *ntepa*, and the informants stated that two could be cut out of a small hide and three out of a large hide. From the offcuts a girl's smaller back apron could be made. The width across the top of an apron was taken to be more or less the span of three hands.

When the skin has been cut out and shaped it is laid on the ground and covered with manure which is left on for about a day. Powdered dry manure is mixed with fresh wet manure for this process (Fig. 19). This is the final step in the preparation, after which the garment is coloured with red ochre.

A woman's front apron, *ntetho*, is always made of goat-skin which is prepared in the same way as the ox-skin, until the cutting process is reached.

After the skin has been cut to the correct pattern it still has to be shaped. Before shaping, however, it is decorated in the following way: the prepared skin is moistened where the working is to begin. A household knife is used to incise a design on the skin (Figs 20, 21). This design covers the entire surface of the

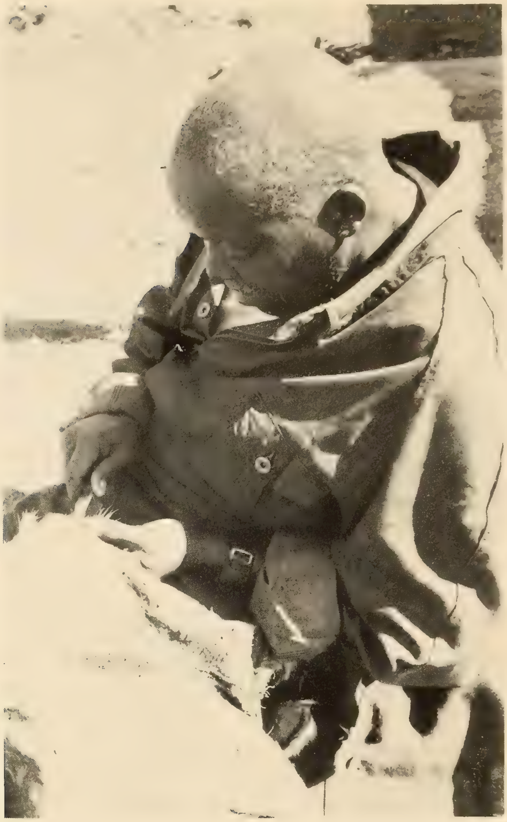


Figure 20

Figure 21

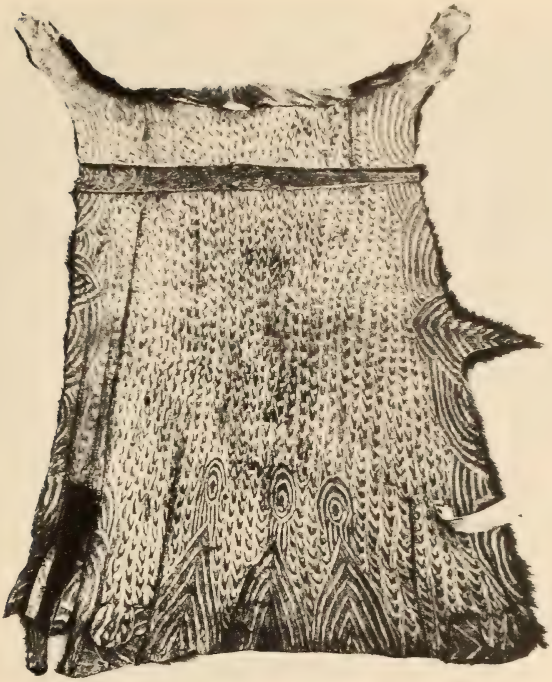


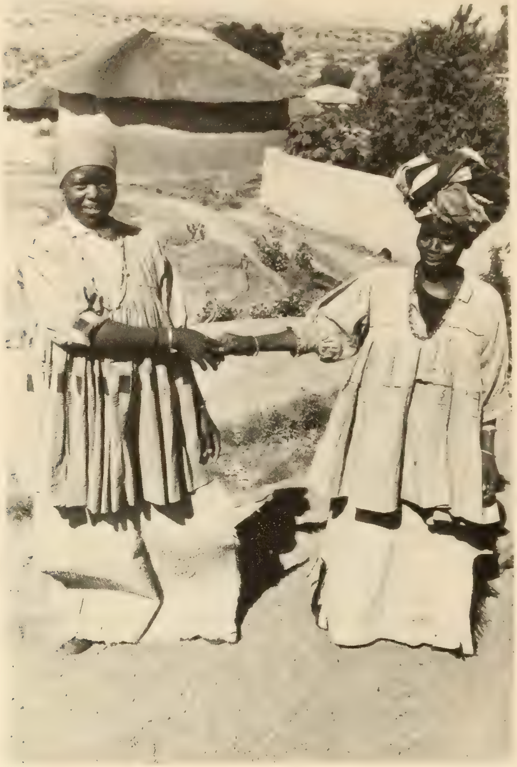
Figure 22

ntetho and when worn the decorated side is on the outside (Figs 22, 23). The knife which is used for doing these designs has to be sharpened at intervals on a whetstone (*selotsu*).

To shape the apron, strips of skin are cut out of it, again using the knife, similar to the way a dressmaker makes darts except that in this case the 'dart' is cut out and the apron sewn together again (Fig. 24). The fibre (*leshika*) which is used is made from the sinew of cattle. It is taken from the carcass while it is still fresh. The dry sinew is then rolled to form a two-ply fibre which is, as was seen in one case, kept in a hussif (*molalachika*) made from 'bobbejaanstert' (*Vellozia equisetoides*) (Fig. 25). An awl is used for making the holes through which the sewing strand is passed (Fig. 26).

The back apron, *ntepa* (Figs 27, 28), is always coloured with red ochre (*letsoko*) which is rubbed into it and gives it a dark red glow. The front apron is sometimes coloured red but it may according to choice have chalk rubbed into it to bring out the incised design more clearly. This gives it a beige colouring. This skinworker purchased red ochre from the near-by Penge Mine, but his supply of chalk came from his family who live near Sekhukhuni (Schoonoord).

The preparation of other types of skins was said not to differ from the technique described. A blanket (*lethebo*) was seen that was made from many different small skins, among them mongoose, springbok and hyrax.



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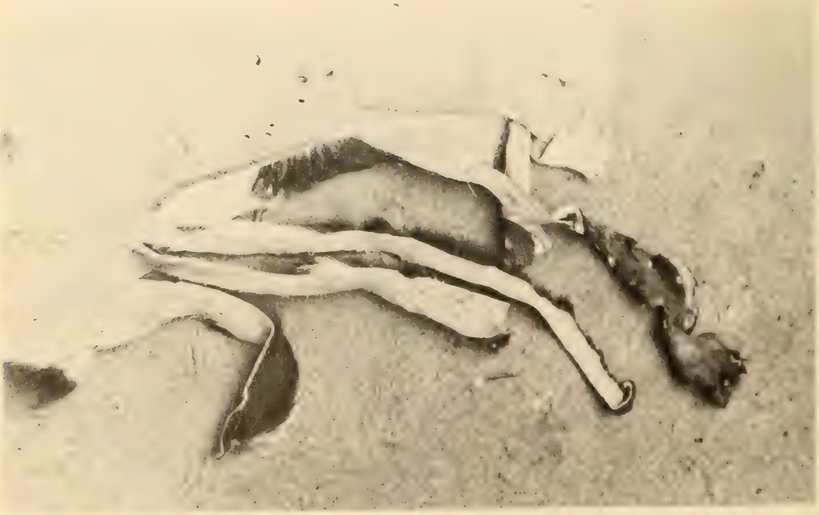

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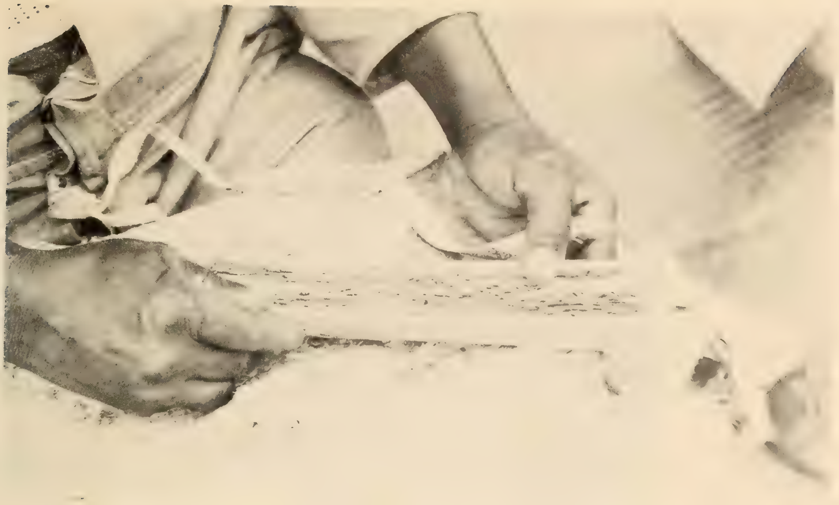

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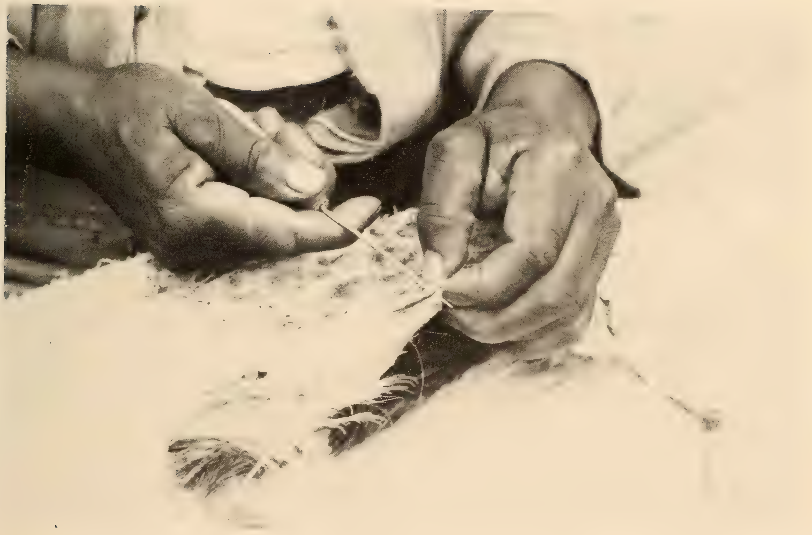

Figure 26

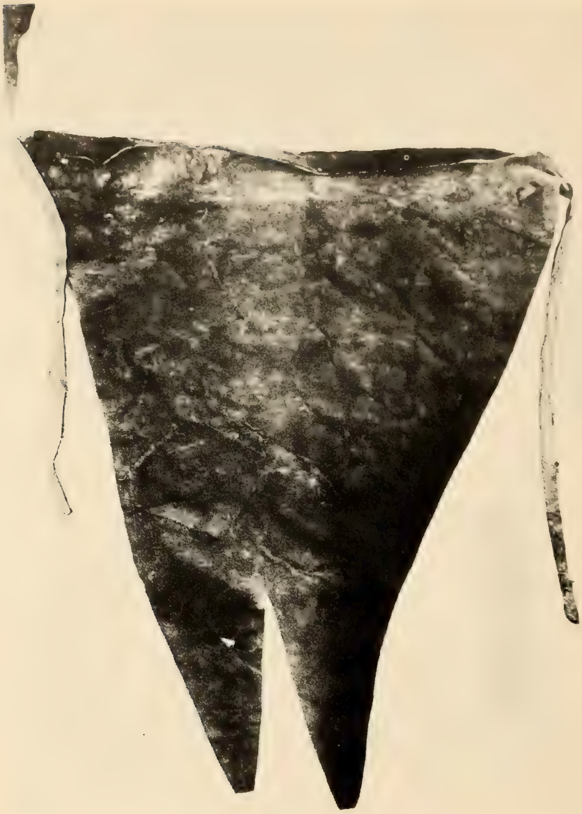

Figure 27

The skinworker said, however, that there was a shorter method of skin-dressing which cut out some stages of the preparation. The main stages of soaking the skin in water, scraping it with an adze, braying with the hands and finally cutting and shaping it, were kept.

ACKNOWLEDGEMENTS

We are indebted to the Secretary for Bantu Administration and Development, the Magistrate, Nebo, the Lebowa Government, and Chief Sekwati for permission to work in the area; to Johannes Mogeng Kgolone for the information given and to him and his assistants for the very excellent demonstration of skin dressing; and to Kgoloko Motlokwe Mompuru and Constable Titus Mdluli who acted as interpreters.

Acknowledgement is made of the financial assistance of the Human Sciences Research Council towards the project of which this study forms a part. Opinions expressed or conclusions reached are those of the authors and should not be regarded as representative of those of the Human Sciences Research Council.

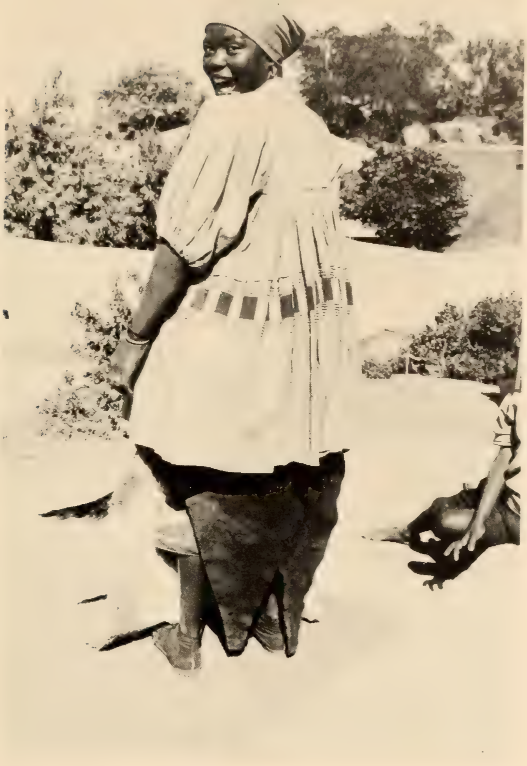

Figure 28

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Fischer, P.-H., Duval, M. & Raffy, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

Thiele, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* Schultze, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika.* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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A NEW SPECIES OF MYSTACOCARIDA (CRUSTACEA) FROM ALGOA BAY, SOUTH AFRICA

By

A. McLACHLAN

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J. R. GRINDLEY

Cape Town Kaapstad

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ISBN 0 949940 59 3

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
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In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
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By

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University of Port Elizabeth

&

J. R. Grindley

Port Elizabeth Museum

(With 1 figure and 2 tables)

[*MS accepted 15 January 1974*]

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INTRODUCTION

Until the revision by Hessler (1972) of the African mystacocarids, all those recorded on the African coasts were regarded as subspecies of *Derocheilocaris remanei* Delamare Deboutteville & Chappius. *D. r. katesae* Noodt was recorded from Durban, South Africa; *D. r. remanei* Delamare Deboutteville & Chappius from Swakopmund, South West Africa; *D. r. remanei* from Luanda, Angola; *D. r. remanei* from Kayar, Senegal, and *D. r. remanei* from the Mediterranean (Hessler 1972).

In the light of the discovery of a distinct species, *D. ingens* Hessler, in Maine, within 260 km of the known range of *D. typica* Pennak & Zinn, Hessler (1972) raised the subspecies of *D. remanei* from Angola and Swakopmund to specific status as *D. angolensis* and *D. delamarei* respectively. Although Hessler (1972) was not able to examine specimens of *D. r. katesae* from Durban he stated that because it was separated from other populations of *D. remanei* by the Swakopmund and Angolan species it probably also warranted specific status.

Hessler (1972) based his differentiation of species on very small morphological differences; differences which were not recognized as specific differences by Noodt (1954). Confirmation of the validity of the specific status of such slightly different morphological forms has now come from the co-occurrence of two closely related species in Algoa Bay, South Africa.

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Here two distinct mystacocarid species, one of them undescribed, have been taken from the same part of the same beach. This is the second recorded overlap of distribution of two mystacocarid species. One has been identified as *D. delamarei* Hessler as it appears to differ from the original description in only the very slightest details. Eight adult specimens of this species have been found in Algoa Bay to date. The other species recorded in Algoa Bay differs significantly from previously described species and is here designated a new species.

MATERIALS

All the specimens described here have been obtained from the intertidal sands of King's Beach, the main bathing beach of Port Elizabeth (33°58′S, 25°39′E) and Bluewater Bay (33°51′S, 25°39′E). Both these beaches are in Algoa Bay. Sand samples were collected during low and mid tides between January and July 1973. The mystacocarids were extracted by means of an Oostenbrink extractor (Oostenbrink 1960) as modified by Furstenberg (personal communication). They were obtained using a sieve with 75 μ mesh and were preserved in 4% formaldehyde.

SYSTEMATIC DESCRIPTIONS

Derocheilocaris algoensis sp. n.

(Fig. 1 A–D)

Holotype—S.A.M. A13535 in the South African Museum, Cape Town.
An adult female from the mid-tide region of King's Beach, Port Elizabeth, South Africa.

Paratypes—S.A.M. A13536 in the South African Museum, Cape Town.
U.S.N.M. 149165 in the United States National Museum, Washington.
Numerous adult males, females and juveniles from King's Beach, Port Elizabeth, South Africa.

Remarks

This species is named after Algoa Bay, its type locality and the only place where it has been recorded to date.

Occurrence

Numerous specimens of different larval stages as well as male and female adults have been obtained from King's Beach. These were found to occur deeper than about 10 cm in the sand between the spring low tide and mid to high tide marks. In some samples they appeared to be the most numerous meiobenthic animals in the deeper sand.

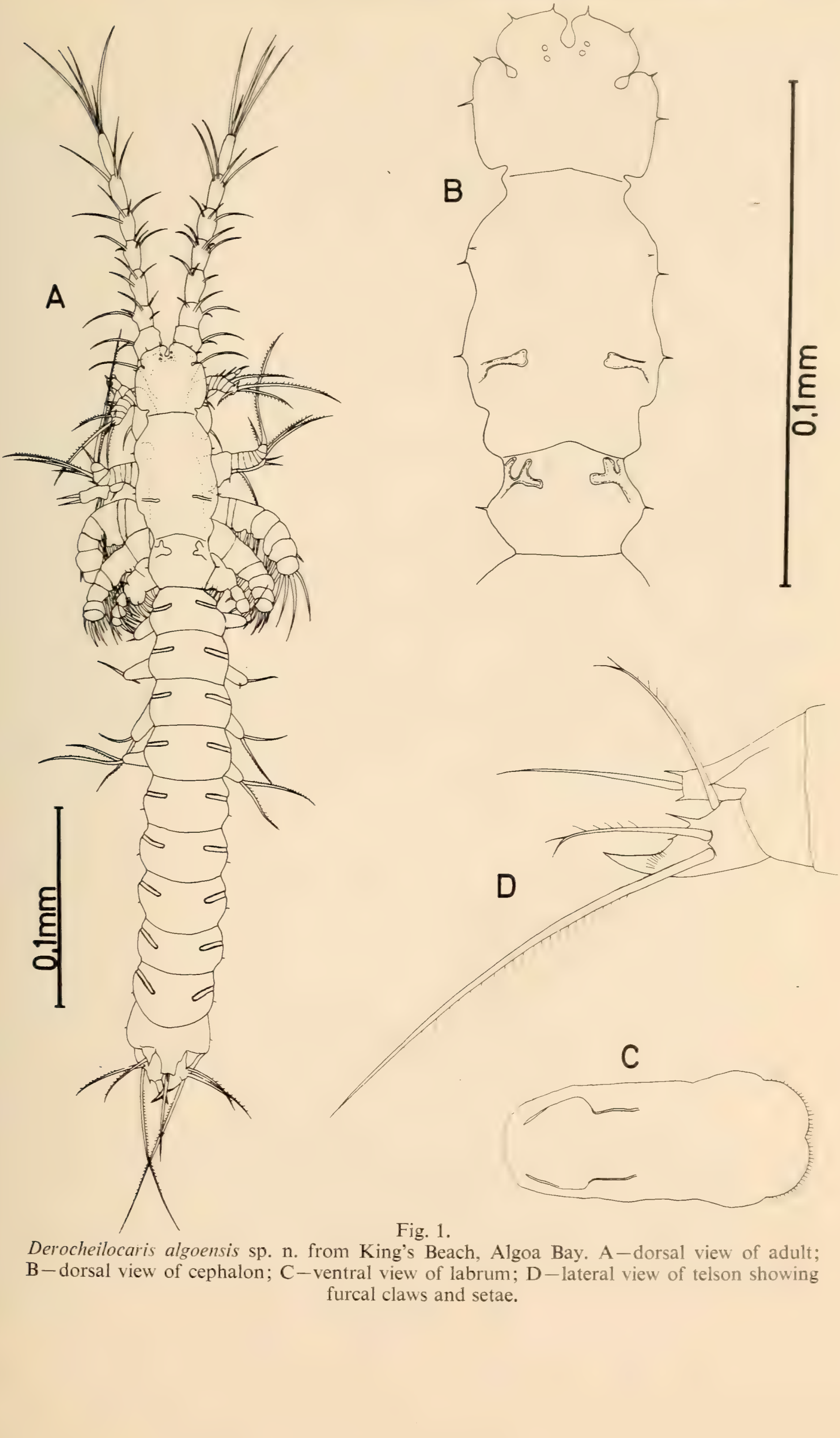

Fig. 1.
Derocheilocaris algoensis sp. n. from King's Beach, Algoa Bay. A—dorsal view of adult; B—dorsal view of cephalon; C—ventral view of labrum; D—lateral view of telson showing furcal claws and setae.

Diagnosis of adult

(All terms are as used by Hessler 1972.)

Anteromedial lobes of antennulary portion of cephalon without medial spines as in *delamarei* (Fig. 1B); sides of antennulary portion of cephalon convex and not converging appreciably posteriorly; posterolateral corners of antennulary portion of cephalon moderately angular; constriction separating antennulary portion of cephalon from rest of cephalon a moderately deep notch in dorsal view; immediately posterior to notch sides of cephalon converge before expanding into antennary region; anterolateral pair of spines in antennary region of cephalon not borne on pronounced protuberances as in *remanei*.

Posterior part of labrum (Fig. 1C) not as expanded as in *D. typica* and with a slight notch in some specimens.

Lateral toothed furrows moderately developed with irregular margins and no distinct teeth.

Distal segment of maxilla 1 with 8 setae.

Endopod of maxilliped with 1 seta on distal segment and 2 setae on penultimate segment.

Supra-anal process (Fig. 1D) terminating in moderate acute process ventral and well-developed acute process dorsal to supra-anal seta; no strongly developed spines around base of acute processes; setules on ventral setae of furcal claws smaller than in *delamarei*; supra-anal seta usually longer than middle or dorsal furcal setae.

The ratios of the lengths of the different furcal and the supra-anal setae to the lengths of the furcal claws were measured as by Hessler (1972) and are given in Table 1. Figures in Table 1 marked with an asterisk differ significantly (p = 0,01) from values for the same ratios in all species described by Hessler (1972).

Table 1.

Ratios of lengths of supra-anal and furcal claw setae to furcal claw lengths in adult *D. algoensis*.

	No	Mean	S.D.	Range
*SSe/F	16	1,01	0,09	0,84–1,18
M/F	16	0,94	0,08	0,77–1,07
D/F	16	0,88	0,11	0,68–1,05
*V/F	16	2,23	0,16	1,95–2,49

F = furcal claw length; SSe = supra-anal seta length; M = middle furcal seta length; D = dorsal furcal seta length; V = ventral furcal seta length; No = number of specimens measured; S.D. = standard deviation;

* indicates ratios significantly different from those for previously described species.

In 15 adults measured, the body length (from the anterior tip of the cephalon to the posterior tip of the furcal claws) averaged 0,39 ± 0,02 mm with a range of 0,37–0,42 mm.

D. algoensis is most quickly identified by (1) the shape of the anterior portion of the cephalon (Fig. 1B), (2) the long (but not as long as *D. delamarei*) ventral furcal setae (Fig. 1D). Table 2 is a summary of some of the more important features whereby *D. r. remanei*, *D. delamarei*, *D. algoensis* and *D. r. katesae* can be distinguished.

Table 2.

Summary of main distinguishing characteristics for four mystacocarids recorded on the African coasts. Compiled from Noodt (1954), Hessler (1972) and the present work.

FEATURE	*D. r. remanei*	*D. delamarei*	*D. algoensis*	*D. r. katesae*
Antero-medial notch of antennulary portion of cephalon	U-shaped	U-shaped with spines	U-shaped	V-shaped
Constriction separating antennulary part of cephalon from rest of cephalon	notched	notched	notched	not notched
Anterolateral spine on antennary part of cephalon	on protuberance	on protuberance	on margin	—
Toothed furrows	well developed	well developed	moderately developed	—
SSe longer or shorter than M and D	shorter	shorter	longer	—
Ventral furcal seta	short	very long	long	long
Spines on supra-anal process	small	large	small	small
Acute process(es) on supra-anal process	ventral to SSe	ventral to SSe	ventral & dorsal to SSe	ventral to SSe

Larvae

A number of larvae corresponding to the later larval stages described by Hessler & Sanders (1966) for *D. typica* have been found during the winter months. It is hoped that at a later stage when a complete series of larval stages has been collected it might be possible to publish a description of the larval development of *D. algoensis*.

Derocheilocaris delamarei Hessler, 1972

Eight adults and a number of larvae were found near and below low tide at King's Beach and Bluewater Bay. They were taken in the surface 10 cm of the sand during late summer. These specimens are immediately distinguishable from *D. algoensis* by their very long ventral furcal setae which bear long setules. They appear to resemble *D. delamarei* in practically all details. The only difference noted is that the ventral furcal setae bear 27–37 setules whereas *D. delamarei* as illustrated by Hessler (1972) bears 48 setules on the ventral furcal setae. Setal length/furcal claw length ratios fall in the same order as recorded for *D. delamarei* (Hessler 1972). The number of setules on the ventral furcal setae of *D. delamarei* as well as the shape of the cephalon in *D. r. katesae* may not be reliable in the published descriptions so that the differences relating to these features may be of limited value. Considering that 2 100 km of coastline separate Swakopmund and Algoa Bay, it is surprising that *D. delamarei* differs so little in form at the end of its known range. The relative rarity of specimens of *D. delamarei* in Algoa Bay might indicate that this is near the eastern limit of the distribution of this species.

DISCUSSION

Two distinct mystacocarid species are here recorded from the same beach. One species, *D. delamarei*, appears to occur in the surface 10 cm of the sand and has only been found in summer, while another species, *D. algoensis*, is plentiful at depths greater than 10 cm in the sand. Algoa Bay is probably near the eastern limit of the range of *D. delamarei*. This is the second recorded overlap between two mystacocarid species.

These two species differ in details so small that, before the publication of Hessler's (1972) review, they would not have been considered sufficient to warrant separate species status. Nevertheless, because these small differences remain distinct, even where the species occur together, they must indicate different species. This therefore confirms the view of Hessler (1972) that mystacocarids are very conservative and that small yet constant differences do constitute specific differences. In this respect the shape of the antennulary portion of the cephalon and the lengths of the supra-anal and furcal claw spines appear to be especially important characteristics.

SUMMARY

An overlap of distribution of two mystacocarid species is recorded from Algoa Bay (33°58′S, 25°39′E). One is an undescribed species, here named *Derocheilocaris algoensis* sp. n. and the other has been identified as *D. delamarei* Hessler. This is the second recorded case of overlap of mystacocarid species and supports the views of Hessler (1972) that small differences between mystacocarids do constitute specific differences.

ACKNOWLEDGEMENTS

This work was assisted by a research grant from the University of Port Elizabeth. We thank Dr J. P. Furstenberg of the Zoology Department of the University of Port Elizabeth for valuable criticism.

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*Not seen in the original.

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A NEW SPECIES OF MYSTACOCARIDA (CRUSTACEA) FROM ALGOA BAY, SOUTH AFRICA

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ANNALS
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ANNALS OF THE SOUTH AFRICAN MUSEUM
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Volume **66** Band
February **1975** Februarie
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PART 1

FAMILY BODOTRIIDAE, SUBFAMILY VAUNTHOMPSONIINAE

By

JENNIFER DAY

Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1),
11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R3,50

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1975

ISBN 0 949940 61 5

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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FAMILY BODOTRIIDAE, SUBFAMILY VAUNTHOMPSONIINAE

By

JENNIFER DAY

Zoology Department, University of Cape Town

(With 15 figures and 1 table)

[*MS accepted 21 June 1974*]

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INTRODUCTION

This is the first in a series of papers on the Cumacea of southern Africa (south of 20°S). The families best represented in these waters are the Bodotriidae and Diastylidae. There are relatively few Leuconidae, Lampropidae and Nannastacidae, while the Pseudocumatidae are numerous, but confined almost exclusively to estuaries, where there are perhaps two species. There are also further specimens of the Ceratocumatidae to be described in a later paper in the series.

Studies on the cumacean fauna of southern African waters are scanty. Stebbing published two papers (1910, 1912) on material sent to him by the South African Museum, mainly describing specimens collected during the voyages of the s.s. *Pieter Faure* from 1898 to 1907. Zimmer (1908) included several South African species in his descriptions of the Deutsches Tiefsee-Expedition material, and later (1921) described a few in the collection of the Zoologisches Museum, Berlin. Since then, Fage (1951) and Jones (1956) have described a few species from this region in the collections of the Belgian Oceanographic Expedition and Atlantide series respectively, and Hale (1953) and Jones (1960) have published on some of the material in the collection of the University of Cape Town. Otherwise, the cumacean fauna of the region is poorly known.

MATERIAL

Some of the more interesting specimens were kindly loaned by Dr Brian Kensley of the South African Museum (SAM)—largely material obtained by the s.s. *Pieter Faure*, which is old and therefore frequently decalcified and damaged. Two specimens of *Vaunthompsonia natalensis* were sent to me by Mr Tim McClurg from the Natal Benthic Survey being carried out by the National Institute for Water Research (NIWR) of the Council for Scientific and Industrial Research (CSIR). The vast majority of specimens, however, was obtained by the Zoology Department of the University of Cape Town (UCT) during an extensive benthic survey of inshore waters from Lüderitzbucht in South West Africa to Inhambane in Moçambique, the cruises being funded by the Oceanographic Research Unit of the CSIR. I am particularly grateful for access to this material.

STATION DATA

The UCT material is numbered according to the area from which it was obtained: WCD (West Coast Dredge) from the border of South West Africa to Cape Agulhas, LBT from the Lambert's Bay Transect, FAL from False Bay, SCD (South Coast Dredge) from Cape Agulhas to the southern border of Natal, NAD (Natal Dredge) from Natal waters, and PED (Portuguese East Dredge) from Moçambique (Fig. 1). 'Coast' indicates material from the NIWR survey, and 'SAM', South African Museum material. The depths and positions of all SAM (*Pieter Faure*) stations have been approximated from charts, since the station data are sketchy, and many depths are not given, or are inaccurate.

METHODS

All the SAM and NIWR material was obtained by dredging. In the UCT survey, heavy-duty dredges and Van Veen grabs of area 0,2 m^2 were used. Some of the LBT material was obtained using a scuba-diver-operated suction device (Christie & Allen 1972). The instrument is a cylinder sampling an area of 0,1 m^2 by 60 cm deep, which is lowered right into the substrate. Different fractions of substrate may then be collected, enabling analysis of fractions from different levels below the surface. The cumaceans were all obtained in the top 10 cm fraction.

Length measurements were in all cases taken from the most anterior point of the carapace to the posterior edge of the telsonic somite, the uropods being omitted from these measurements.

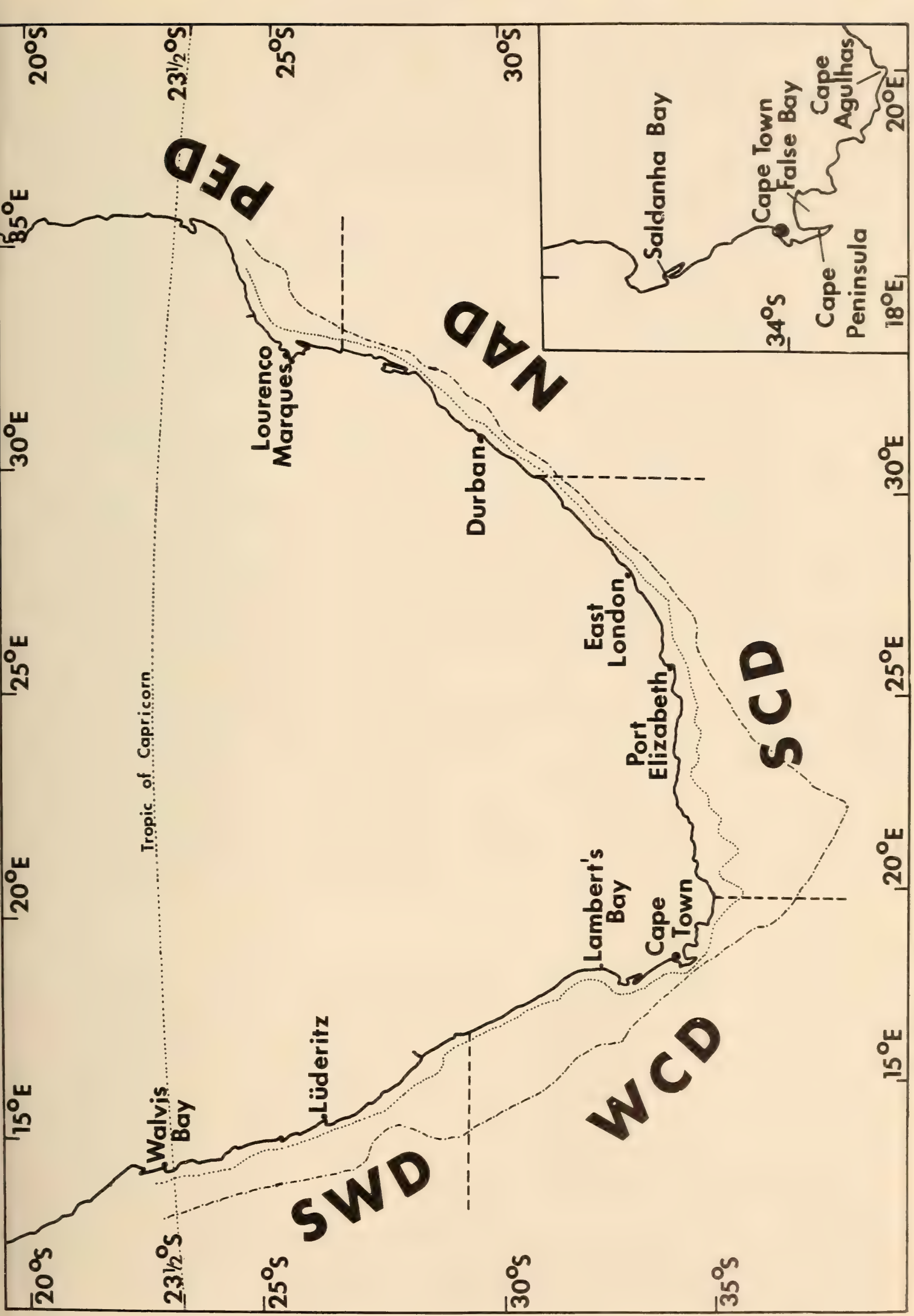

Fig. 1. Southern Africa south of 20°S: .... 100 m depth contour; .–.–.– 500 m depth contour. Inset: south-western Cape.

STRUCTURE AND TERMINOLOGY

The terminology used by authors who are familiar with a group is frequently confusing to those who are dealing with it for the first time. Below is a brief account of the structure of the Cumacea, and the terminology used to describe it. For a fuller description, the reader is referred to Jones (1963), whose terminology is adopted in the present series, particularly in the use of the term 'somite' as a metameric segment of the body, and 'segment' as a podomere of the appendages.

The Cumacea are typical Malacostraca, having 19 body segments or *somites*, each of which may bear a pair of appendages. The *head* region consists of five somites, bearing from the anterior end two pairs of antennae, a pair of mandibles and two pairs of maxillae. There are eight *thoracic somites*, the anterior three bearing maxillipeds, and the posterior five (the *pedigerous somites*) bearing pereiopods. The *abdomen*, of six *pleon somites*, may have up to five pairs of pleopods in the male, and none in the female. The sixth abdominal somite bears a pair of uropods. A *telson* is present in some families, and in others it is fused with the last abdominal somite which is known as the *telsonic somite*.

A well-developed *carapace* is present, fused not only to all five head somites, but also to three, four, five or six thoracic somites. It is bowed laterally to cover the branchial chambers, and is produced anteriorly to form *pseudorostral lobes*, below which is the exhalent opening of the branchial chamber. The two lobes together are known as the *pseudorostrum*. Antero-laterally the carapace is frequently notched to accommodate the first antenna—the *antennal notch*—with a sharp point, the *antero-lateral angle*, below it. Dorsally, if visual elements are present, they are usually fused into a single median *eye*, frequently pigmented, with a variable number of lenses. The eye is situated on the *eyelobe*, a median projection of the carapace anteriorly between the pseudorostral lobes. The carapace may be quite smooth, but is often ornamented with tubercles, spines or other projections, or is sculptured into median and/or lateral keels or *carinae*. The free thoracic and abdominal somites may also be carinate.

APPENDAGES

Antenna 1 (antennule) consists of three basal segments bearing two flagella. The main *flagellum*, of up to six segments, carries a number of sensory filaments or *aesthetascs*, which are usually annulated. The *accessory flagellum* may have up to four segments, or may be wanting.

Antenna 2 is rudimentary in the female, but may reach the entire length of the body in the male, where it may be used for sensing the presence of the female, or for clasping her during copulation.

Mandibles are formed from a single segment, and are normally crescent-shaped.

Maxilla 1 (maxillule) is rudimentary, but may bear one or two epipodal filaments reaching into the branchial chamber.

Maxilla 2 (maxilla) is also rudimentary.

The *thoracic appendages* are typical stenopodous limbs. *Exopods*, some of which may be rudimentary, are always found consecutively on at least two of these limbs from maxilliped 3 to pereiopod 4 inclusive. The maximum number is five, and there are usually more in the male than the female. The exopods consist of a *basal segment*, sometimes expanded into a laminar plate, and a variable number of distal segments which usually carry long plumose setae. Well-developed exopods assist considerably in swimming. The *endopod* of a thoracic appendage is typically divided into seven *segments*. These are named (from the proximal end) the *coxa*, *basis*, *ischium*, *merus*, *carpus*, *propodus* and *dactyl*.

Maxilliped 1 normally consists of a seven-segmented endopod and an epipodite developed into a series of plates or lobes which function as the *gill*.

Maxilliped 2 is also normally seven-segmented. The coxa of ovigerous females is produced to form a *rudimentary oostegite*, bearing filaments which extend into the brood chamber and fan the developing embryos.

Maxilliped 3, always seven-segmented, usually bears a well-developed exopod. The outer distal portion of the basis is frequently expanded, and the basis forms a shield protecting the mid-ventral region of the thorax.

Pereiopod 1, always bearing an exopod, is seven-segmented, and is frequently elongated, reaching beyond the anterior end of the pseudorostral lobes.

Pereiopods 2 to 5 may or may not bear exopods, and are normally seven-segmented, although in some genera the ischium of pereiopod 2 is fused with the basis.

The male may bear up to five pairs of biramous *pleopods*. These may be rudimentary, but if fully developed consist of a basal segment, a 1-segmented *inner ramus* and a 2-segmented *outer ramus*. The distal ends of the rami are frequently supplied with a large number of plumose setae used in swimming.

The *uropods*, also biramous, consist of a 1-segmented *peduncle*, a 2-segmented *exopod* and an *endopod* which may consist of one, two or three segments. These appendages form the forked tail characteristic of all Cumacea.

SEXUAL DIMORPHISM

The Cumacea exhibit considerable sexual dimorphism. The sexual differences include small details such as the sculpturing and degree of armature of the exoskeleton, but most other more basic differences can be attributed to characters allowing greater swimming capacity in the male, and the presence of a *marsupium* or brood pouch in the female. Distinguishing male from female is important, since several characters of the males of some genera are the same as the female characters of another. Determination of sex is not always easy, especially in an immature animal, but the following may be helpful as a guideline:

The *adult male* has between zero and five pairs of pleopods, usually setiferous, and the second antennae extend a considerable distance along the body. Thoracic exopods are frequently flattened and expanded, the antero-lateral angle rounded or obliterated, and serrations of the carapace reduced or absent.

The *subadult male* has a full complement of pleopods, not yet setiferous, and the second antennae are still developing. Sculpturing of the exoskeleton is often midway between the condition of the adult male and the female.

The *ovigerous female* is distinguished by the presence of a *marsupium*. The coxae of maxilliped 3 and pereiopods 1 to 3 develop *oostegites*, forming a large ventral brood chamber in which the eggs are visible during the later stages of development.

The *adult female* differs from an ovigerous one only in the absence of a marsupium.

The *manca*, the larval stage at which the animals are released from the marsupium, is characterized by the absence of the last pair of pereiopods.

The *juveniles* may be recognized, apart from their small size, by the absence of sexual dimorphism.

The majority of *males* and *females* in most collections are intermediate between the fully adult and juvenile stages, and although some sexual differences are present, they are not always easily determined. For example, in many bodotriids, the lateral plates of the pedigerous somites differ even in young males and females. However, this type of character is variable, and must be determined anew for each genus or species. One distinguishing characteristic which holds true for many (but not all) genera is that the male tends to have more pereiopods bearing exopods than does the female.

SYSTEMATICS

The Cumacea, being a rather homogeneous group, have few characters which divide them obviously into families. Thus two main schemes have been used to separate them. The one, detailed by Stebbing in 1913, now has 27 families. The other more commonly adopted scheme has seven families. Although neither of these systems is ideal, the latter is less cumbersome and will be adopted in the present series of papers.

Family **Bodotriidae** Scott, 1901

Diagnosis

No free telson. Pleopods with an outer process to the inner ramus—usually five pairs, but may be two (*Mancocuma*) or three (*Leptocuma*). Mandibles normal (i.e. not broad at base). Endopod of uropod 1- or 2-segmented. Branchial apparatus without gill plates or supports.

The family was divided by Hale (1944) into two subfamilies, the Bodotriinae and Vaunthompsoniinae. The Bodotriinae are characterized by having exopods limited to the third maxillipeds and first pereiopods in both sexes. The South African representatives of the subfamily will be dealt with in the second paper of this series.

Subfamily **Vaunthompsoniinae** G. O. Sars, 1879

Diagnosis

Bodotriidae with exopods on pereiopods other than the first pair.

KEY TO THE SOUTH AFRICAN SPECIES OF VAUNTHOMPSONIINAE

It should be noted that this key will separate all species found to date in southern African waters, but will *not* necessarily distinguish them from species from other areas.

1 Exopods present on pereiopods 1 and 2 only (♂ and ♀)................................ *Pseudosympodomma africanum* (Fig. 2)
– Exopods present on pereiopods 1 to 3 (♂ and ♀)................................2

2 Exopods of pereiopods 2 and 3 rudimentary..3
– Exopods of pereiopods 2 and 3 well-developed; ♂ with exopod on pereiopod 4..........5

3 Maxilliped 3 with basis not at all produced distally..*Cumopsis robusta* sp. nov. (Figs 5, 6)
– Maxilliped 3 with basis produced distally..4

4 Pereiopods 2 and 3 with exopods 1-segmented.........*Heterocuma africanum africanum*
– Pereiopods 2 and 3 with exopods 2-segmented.. *Heterocuma africanum intermedium* (Figs 3, 4)

5 Maxilliped 3 with basis not at all produced distally..6
– Maxilliped 3 with basis produced distally..9

6 Eye absent; carpus of maxilliped 3 inserted half way along length of merus; merus expanded externally .... *Hypocuma dentatum* sp. nov. (Figs 7, 8)
– Eye present; carpus of maxilliped 3 not expanded, and inserted at distal end of merus....7

7 Serrated middorsal carina present in ♀.......................... *Vaunthompsonia cristata*
– No middorsal carina present in female..8

8 Merus of maxilliped 3 longer than carpus; first segment of exopod of uropod less than half length of first segment of endopod........ *Vaunthompsonia natalensis* sp. nov. (Figs 9, 10)
– Merus of maxilliped 3 shorter than carpus; first segment of exopod of uropod nearly as long as first segment of endopod.......................... *Vaunthompsonia* sp. (Fig. 11)

9 Carapace of ♂ and ♀ with middorsal serrations; telsonic somite produced between uropods for at least ⅓ its length 10
– Carapace of ♀ at least with no middorsal serrations; telsonic somite little produced between uropods.................................... *Bathycuma datum* sp. nov. (Fig. 15)

10 Peduncle of uropod longer than telsonic somite; antenna 1 of adult ♂ very large, with many setae .... *Bathycuma natalense* (Figs 13, 14)
– Peduncle of uropod shorter than telsonic somite; antenna 1 of ♂ unmodified............ *Bathycuma capense* (Figs 12, 13)

Pseudosympodomma Kurian, 1954

Generic diagnosis

Eyelobe narrowly linguiform with a cluster of lenses anteriorly—more in male than female. Pseudorostral lobes extending anteriorly but not meeting in front of elongated eyelobe. All pedigerous somites exposed. Basis of maxilliped 3 distally produced. Pereiopods 1 and 2 with free exopods in both sexes; adult male sometimes with a small ridge in position of exopod of pereiopod 3. Male with five pairs of pleopods. Endopod of uropod 2-segmented.
Type species *P. indicum* Kurian, 1954, from India, 'in weeds, 0,2 fm'.

*Pseudosympodomma africanum** (Stebbing, 1912)

Fig. 2

Sympodomma africanus Stebbing, 1912: 138, pl. L.
non *Sympodomma africanum:* Hale, 1928: 40, figs 9–10; 1944: 284, fig. 30.

Records

SAM A4331,	*Pieter Faure* 10782:	29°49′S/31°08′E	85 m	1♀	10,9 mm	
SAM A597,	*Pieter Faure* 17643:	34°24′S/17°58′E	370 m	1♀ adult	15,7 mm	PARATYPE
SAM A598	*Pieter Faure* 17643:	34°24′S/17°58′E	370 m	1♂ subadult	15,7 mm	
PED 23 X	22.8.1964	26°00′S/33°05′E	135 m	1 manca	4,3 mm	

Note: In his description of *S. africanum*, Stebbing gave the depth as 805 m. In fact, if the distance of 12½ miles from Cape Natal (*Pieter Faure* log) is correct, then the depth can be no more than 400 m in any direction, according to present-day charts. The bearing also appears to be the reciprocal of the normal bearings in the log, as 'Cape Natal N 3/4 E 12½ miles' is practically in the surf zone.
Holotype designated by Stebbing (1912) as *Sympodomma africanus*, *Pieter Faure* 17643 (as above), subadult male, 18,0 mm. British Museum (Natural History).

Description

Adult female, length 15,7 mm, paratype. Broken in two, but otherwise undamaged.

Carapace faintly tubercular, nearly twice as long as deep; median carina with three very large, anteriorly-directed teeth on the anterior part (Fig. 2A). Eye present, lenses distinct—seven above and seven below (Figs 2B, 2C). Eyelobe elongated, pseudorostral lobes not meeting. Antennal notch fairly shallow, semicircular; antero-lateral angle almost rectangular. All pedigerous somites visible above. Sternite of fourth pedigerous somite with anteriorly-directed tooth. Carapace as long as free thoracic somites. Cephalothorax equal in length to first four abdominal somites. Pedigerous somites with faint lateral carinae; two pairs of lateral carinae along length of abdomen. Telsonic somite produced between uropods for nearly ⅓ its length.

Antenna 1 (Fig. 2D) geniculate between segments 1 and 2. First segment large, slightly expanded laterally, equal in length to next two segments. Flagellum 2-segmented with two terminal setae. Accessory flagellum 2-segmented, equal in length to first segment of flagellum.

Maxilliped 3 (Fig. 2E) with basis 2½ times length of remaining segments, widely expanded at distal end, with four spines along the outer edge and two apical ones. Inner edge with a row of small denticles along its length. Remaining segments almost equal in length, ischium slightly the longest. Merus expanded slightly externally and carpus internally. Exopod small, basal segment less than ⅓ length of basis.

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*The words 'omma' (Gr.), an eye, and 'cuma' (Gr.), an embryo, are grammatically neuter, hence *Pseudosympodomma africanum*, *Bathycuma natalense*, etc.

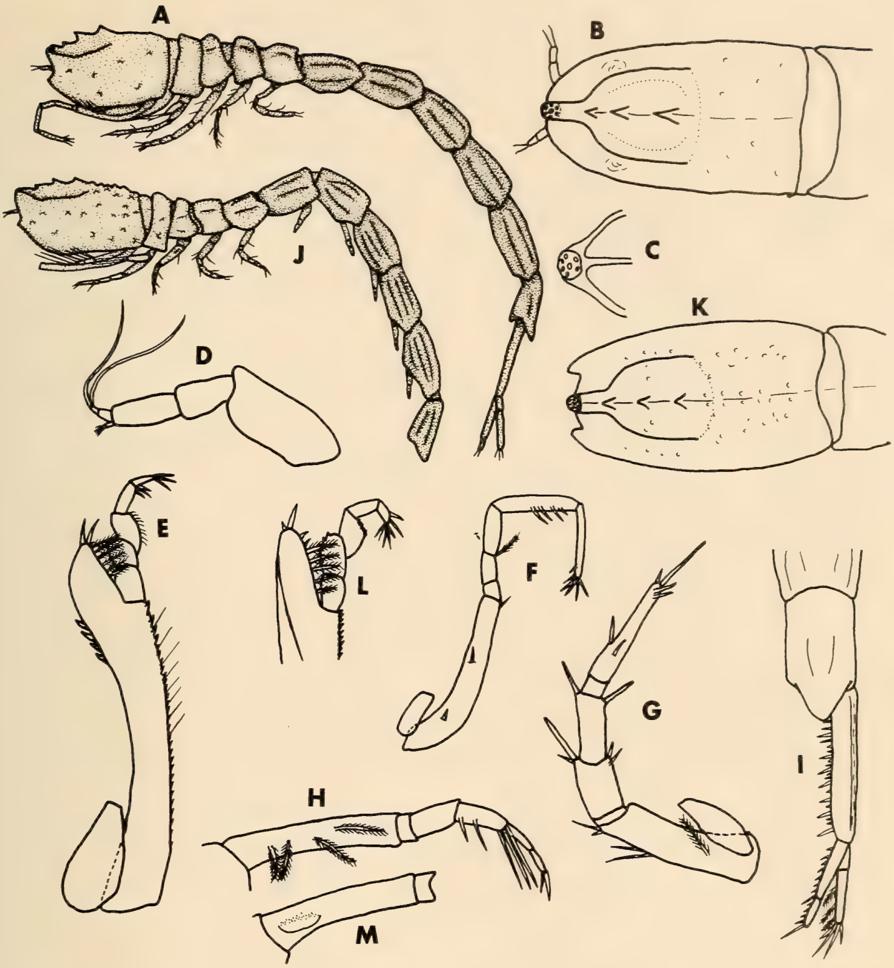

Fig. 2. *Pseudosympodomma africanum* (Stebbing, 1912)

Adult female, paratype, 15,7 mm: A, lateral view; B, dorsal view of carapace; C, ventral view of eyelobe; D, antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, telsonic somite and uropod.

Subadult male, 15,7 mm: J, lateral view; K, dorsal view of carapace; L, distal portion of maxilliped 3; M, proximal segments of pereiopod 3.

Pereiopod 1 (Fig. 2F) fairly stout. Basis equal in length to next four segments. Ischium short. Propodus and dactyl long, subequal, each equal in length to merus plus carpus. Exopod small, basal segment not much more than a quarter length of basis.

Pereiopod 2 (Fig. 2G) stout. Basis equal in length to next four segments. Ischium $\frac{1}{3}$ as long as broad. Merus and carpus subequal. Dactyl equal to merus plus carpus and bearing a number of scattered spines. Basal segment of exopod $\frac{2}{3}$ length of basis.

Pereiopod 3 (Fig. 2H) more slender. Basis equal in length to rest of leg. Ischium small, half as long as broad. Merus and carpus subequal. Carpus just longer than propodus, which is again slightly longer than dactyl. No exopod.

Peduncle of uropod (Fig. 2I) just longer than telsonic somite with 20 unequal spines along inner edge. Endopod slightly longer than exopod and about $\frac{2}{3}$ length of peduncle; first segment twice length of second, with eight small spines on inner margin, second with four, and one terminally. Exopod with first segment half the length of second, and unarmed. Second segment with three plumose setae on the inner margin and four terminal spines.

Subadult male, length 15,7 mm. In poor condition, uropods and parts of some thoracic appendages missing. As in the female, except as follows: teeth on middorsal carina less elevated, and followed by a row of uneven tubercles, the dorsal outline thus appearing uneven. Tubercles scattered over the rest of the carapace (Figs 2J, 2K). Antennal notch much shallower, antero-lateral angle less obvious. Ventral margin faintly dentate below the angle for about $\frac{1}{3}$ its length. Sternites of fourth and fifth pedigerous somites with an anteriorly-directed tooth in the midline. Abdominal somites with three pairs of carinae.

Distal prolongation of maxilliped 3 (Fig. 2L) narrower than in female, with four distal spines. Inner edge more spinous. Merus and carpus further expanded, these edges dentate.

Pereiopods as in female. Pereiopod 3 (Fig. 2M) without a free exopod, but with a slight swelling along the outer edge of the basis for about $\frac{1}{3}$ its length.

Five pairs of pleopods present.

Uropods missing. Telsonic somite of holotype male broader than that of female. Stebbing's figure of uropods of holotype as in female of present collection, but with greater armature.

Remarks

Stebbing (1912) described the species from a single subadult male, and the above specimens differ from his description only as follows: carapace of holotype less tubercular; distinct individual lenses present in eye of female, but eye of male as figured by Stebbing. Maxilliped 3 of holotype with merus and carpus slightly more expanded, with setae and not denticles along expanded edges. Stebbing figured the basal segment of antenna 1 as geniculate. The antennae of the holotype are missing, but in the present specimens the antenna is geniculate between the first and second segments.

In 1912 Stebbing erected a new family, the Sympodommatidae, with the single genus *Sympodomma* to receive four species—*Vaunthompsonia anomalum* (G. O. Sars, 1871), *Heterocuma weberi* Calman, 1905, *Heterocuma diomedaea* Calman, 1912 and a new species, *Sympodomma africanum*. The main distinguishing feature of the new family and genus was the presence of exopods on pereiopod 3 in both sexes. These were obviously present (according to descriptions in the literature) in the first three species, but he says of *S. africanum* (one subadult male) that: 'exopods to the third pair were not satisfactorily made out, but may be presumed, as they occur in both sexes of the allied Japanese species.'

In addition to the holotype, I have examined four specimens which undoubtedly belong to Stebbing's *S. africanum*. One is a paratype, a subadult female, from the type locality with the same station data and museum number as the holotype. Another specimen, a subadult male from the same locality but with different station data, has a swelling in the expected position of the exopod of pereiopod 3, but this is fused to the basis along its entire length. Unfortunately the holotype now consists of little more than an empty carapace, three badly damaged and limbless thoracic somites and several abdominal somites, so that the pereiopods in question could not be examined. Neither of the females nor the manca had the slightest trace of an exopod on these limbs.

In 1954 Kurian erected a new genus, *Pseudosympodomma*, to receive a new Indian species, *P. indicum*, which has exopods on pereiopods 1 and 2 only in both sexes. He suggested that *Sympodomma africanum* might be referable to the new genus. Owing to the lack of an exopod on pereiopod 3 of the present specimens, Stebbing's *S. africanum* must now be referred to the genus *Pseudosympodomma*.

The two species of the genus may be distinguished as follows: the pseudorostral lobes and eyelobes of *P. indicum* are relatively longer than those of *P. africanum*. *P. indicum* has a 3-segmented accessory flagellum, while that of *P. africanum* is 2-segmented. In *P. indicum* the exopod of maxilliped 3 is less than a quarter the length of the basis; the prolongation of the basis is narrower and extends well beyond the merus. The last two segments of the first pereiopod are longer and more slender. The two segments of the endopod of the uropod are subequal, the two rami are of equal length, and the first segment of the exopod is only a quarter the length of the second. In the description of *P. indicum*, no mention is made of the teeth on the sternites of the pedigerous somites.

The two genera *Sympodomma* and *Pseudosympodomma* are very similar in general appearance, in distinctive features such as the large teeth or incisions on the dorsal carina, and the presence of teeth on the thoracic sternites of several species. Thus the genera are closely related, and the single feature distinguishing between them is the presence or absence of exopods on pereiopod 3. In the female this is quite clear, but in the male even this character is less distinctive due to the small protuberances on the bases of these legs. Thus the generic diagnosis of *Pseudosympodomma* has been expanded to accommodate *P. africanum*.

It should also be noted that Hale (1928, 1944, 1949) had some specimens which he considered to be *S. africanum*. Later, being unable to obtain more material, he erected a new species, *Sympodomma ?incerta* Hale, 1949. It is very similar to *P. africanum* in external appearance, but due to the presence of an obvious exopod on pereiopod 3 of the male, Hale's query may be removed, and the species becomes *Sympodomma incertum*.

Distribution of Pseudosympodomma

P. indicum is found in shallow Indian waters (Kurian 1954), and *P. africanum* from Natal to Cape Point at depths from 85 to 370 m. Thus the genus falls into the Indo-Pacific faunal group.

Heterocuma Miers, 1879

Generic diagnosis

Vaunthompsoniinae with the first pedigerous somite visible dorsally. Telsonic somite not produced. Eye present. Basis and merus of maxilliped 3 distally produced. Pereiopods 2 and 3 with rudimentary exopods in both sexes. Endopod of uropod 2-segmented. Male with five pairs of pleopods.
Type species *H. sarsi* Miers, 1879, from Korea and Japan.

KEY TO THE SPECIES OF *HETEROCUMA*

1 Pereiopods 2 and 3 with exopods 2-segmented.....................................
H. africanum intermedium (Fage, 1924)—West and South Africa
– Pereiopods 2 and 3 with exopods 1-segmented.....................................2

2 Pleon segments carinate...3
– Pleon segments not carinate...4

3 First segment of endopod of uropod shorter than second..........................
H. sarsi Miers, 1879—Korea and Japan
– First segment of endopod of uropod longer than second. . *H. andamani* Kurian, 1954—India

4 Endopod of uropod distinctly shorter than peduncle...............................
H. africanum africanum Zimmer, 1921—India, West and South Africa
– Endopod of uropod just longer than peduncle.......... *H. armatum* Kurian, 1954—India

Heterocuma africanum intermedium (Fage, 1924) n. comb.
Figs 3 (♀), 4 (♂)

Heterocuma intermedia Fage, 1924: 364, fig. 1.
Heterocuma africana: Jones, 1956: 194 (?pars); 1960: 172.

Records

WCD 99 R	32°05′S/18°17′E	2.7.1961	27 m	Sandy shell	1♂ adult	18,4 mm
SCD 151 C	34°55′S/21°26′E	21.2.1960	91 m	Sand	1♀ adult 1♀ ovig.	19,1 mm 24,8 mm
SCD 293 F	33°04′S/27°57′E	6.2.1962	84 m	Sandy shell	1♀ ovig.	22,4 mm
FAL (False Bay)	34°S/18°E		15–77 m	Sandy shell	15 records: 2 adult ♂ 1 subadult ♂ 2♂ 3♀ ovig. 8♀ adult 5♀ 5 manca	 18,2–18,4 mm; 19,3 mm; 7,9–9,4 mm; 19,2–23,2 mm; 17,6–21,6 mm; 7,4–11,0 mm; 4,0–5,8 mm (1 adult ♂, 1 ♀ ovig. and 2 ♀ adult identified by Jones 1960)

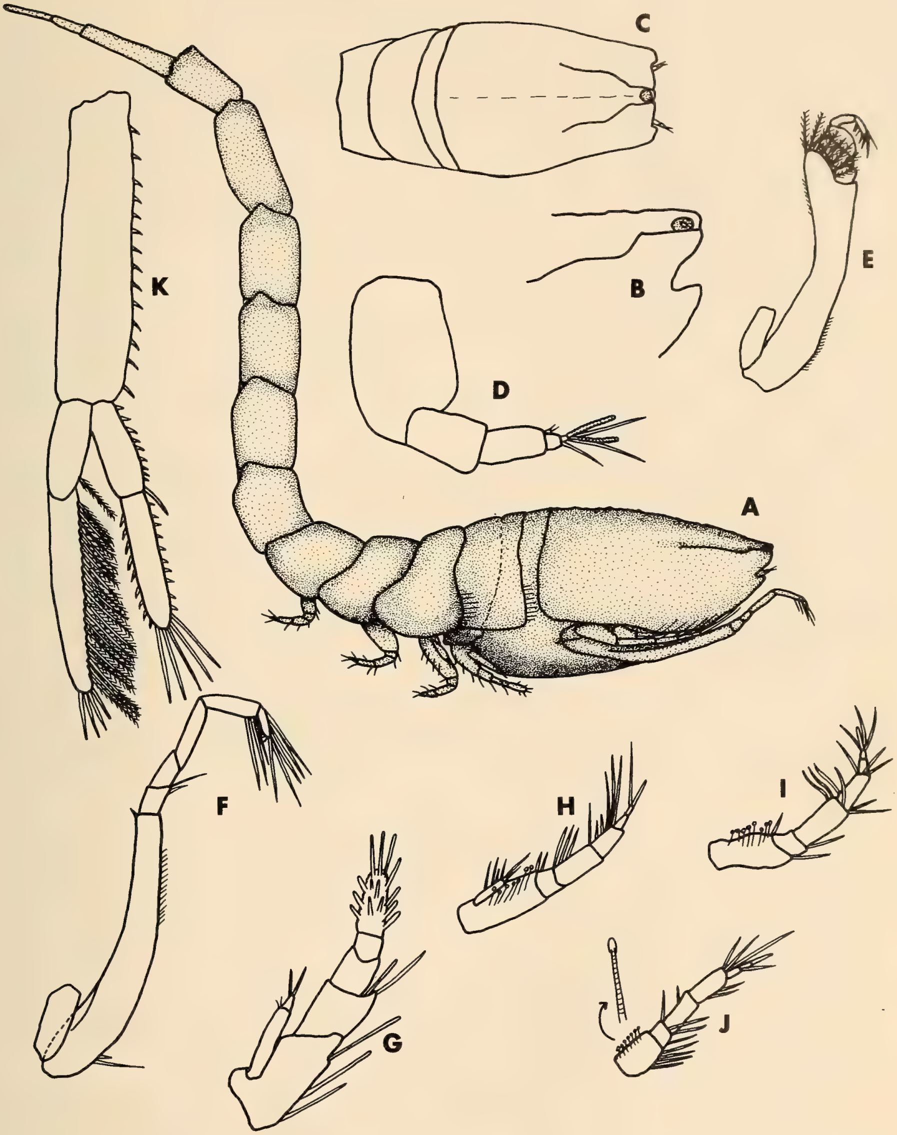

Fig. 3. *Heterocuma africanum intermedium* (Fage, 1924)
Ovigerous female, 23,2 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, pereiopod 4; J, pereiopod 5; K, uropod.

Holotype designated by Fage (1924) as *Heterocuma intermedia*; Museum National d'Histoire Naturelle, Paris.

Description

Ovigerous female, length 23,2 mm. Carapace twice as long as deep with a faint mid-dorsal carina. In lateral view (Fig. 3A), mid-dorsal line irregular and faintly arched posteriorly. Antennal notch deep, antero-lateral angle acute (Fig. 3B). Carapace just shorter than remaining free thoracic somites. Thorax and abdomen subequal. No lateral plates or carinae on abdomen. Eye present with single lens faintly visible on either side. Pseudorostral lobes not meeting anterior to eyelobe (Fig. 3C).

Antenna 1 (Fig. 3D) with basal segment very much expanded, being twice as long and twice as broad as second segment. Second and third segments subequal, second broader. Flagellum 2-segmented, first twice as long and as broad as second which carries a number of terminal setae and two aesthetascs. Accessory flagellum minute, 1-segmented.

Maxilliped 3 (Fig. 3E) with well-developed broad distal prolongation of the basis. Ischium normal, merus dilated externally and carpus internally. Propodus and dactyl subequal. Basal segment of exopod less than a quarter length of basis.

Basis of pereiopod 1 (Fig. 3F) a quarter as long again as rest of leg. Ischium and merus subequal, as are carpus and propodus. Dactyl half length of propodus. Basal segment of exopod about a quarter length of basis.

Pereiopod 2 (Fig. 3G) very stout—basis half as long as broad. Ischium fused with basis. Dactyl with a large number of spines. Exopod large, as long as the basis, with a small but obvious second segment.

Pereiopod 3 (Fig. 3H) more slender, with exopod half length of basis, and having a small second segment.

Pereiopods 4 and 5 (Figs 3I and 3J) without exopods. Third to fifth pereiopods all furnished with distinctive knobbed setae on the bases.

Peduncle of uropods (Fig. 3K) half as long again as telsonic somite, with one row of 14 small spines on the inner edge. Exopod equal in length to peduncle, with first segment half as long as second. First with a single plumose seta, second with about 20, and four short terminal spines. Endopod $\frac{4}{5}$ length of peduncle, first segment about $\frac{3}{4}$ length of second with nine small and one large terminal spines on the inner edge. Second segment with 9–10 small spines on inner and outer edges, and five terminal spines of equal length.

Note: a single female from False Bay has a particularly well-marked row of tubercles on the mid-dorsal line of the carapace, and carinae running down the length of the abdomen on either side of the mid-line. Otherwise it corresponds with the above description.

Adult male, length 18,4 mm. As the female, except as follows: carapace with much less deeply indented antennal notch, antero-lateral angle almost obsolete (Fig. 4B). Thorax equal in length to next five abdominal somites (Fig. 4A). As is typical for the family, the thoracic sideplates are well developed, that of the

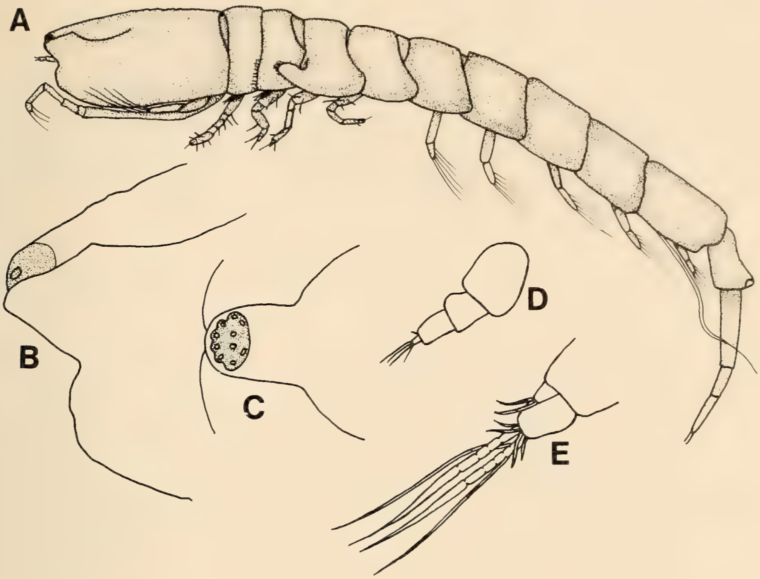

Fig. 4. *Heterocuma africanum intermedium* (Fage, 1924).
Adult male, 18,4 mm: A, lateral view; B, detail of anterior end of carapace; C, detail of eyelobe in dorsal view; D, antenna 1; E, distal segments of antenna 1.

fourth pedigerous somite having a prominent linguiform anterior projection. The armature of the peduncle of the uropods is more pronounced, having about 50 small, closely-packed spines in two rows along the inner edge. The single subadult male from the west coast differs from the adult males only in that the thoracic sideplates and uropodal armature are not fully developed, and the eye has 10 distinct lenses on the dorsal surface (Fig. 4C). Antenna 1 (Fig. 4D) is somewhat shorter in the male, and the flagellum is 1-segmented (Fig. 4E).

Distribution

Tropical West Africa (Fage 1924, 1950, 1951; Jones 1960—part); False Bay and south-west coast of South Africa (Jones 1960).

Heterocuma africanum africanum Zimmer, 1921

Heterocuma africana Zimmer, 1921: 129, figs 25–27. Kurian, 1954: 294, fig. 7.

Records

NAD 86 G	29°10′S/31°51′E	29.7.1964	43 m	Sand	2 ♀ adult	10,4–11,2 mm;
					1 ♂	6,8 mm

Holotype designated by Zimmer, 1921 from West Africa, one subadult male. ?Zoologisches Museum, Berlin.

Description

The single sample from Natal is of interest in that although generally the specimens are very similar to *H. africanum intermedium*, they have short, 1-segmented exopods on pereiopods 2 and 3. The eyes of the single male and both females have lenses similar to those shown in Figure 4C. Although the females are adult, they are only about half the size of comparable specimens from False Bay. The carapace has no trace of a carina.

Distribution

Tropical West Africa (Zimmer 1921; Jones 1956—part); India (Kurian 1954); Natal.

Remarks

Heterocuma africanum was described but poorly figured by Zimmer (1921) from an immature specimen collected together with many juveniles from Freetown in Sierra Leone. Fage (1924) described *H. intermedium* from Rio do Oro, from Goreé (1950) and from Darsen and Annobon Islands (1951). Jones (1956) examined many specimens from the coast of West Africa, and equated Fage's *H. intermedium* with *H. africanum* due to the fact that Zimmer obviously described the latter from an immature specimen. More recently, Jones (1960) identified several specimens (now in the present collection) from False Bay and Dassen Island as *H. africanum*. These are indicated in the records above. Undoubtedly the two forms are very similar in most respects, but they are in fact distinguishable by the nature of the exopods of the second and third pereiopods. In Zimmer's specimen, they were 'in the form of short cylinders', while Fage (1924) specifically mentions 'the greater size and the division into two articles of the exopods of the second and third pereiopods'. Kurian (1954) identified two adult specimens (7–8 mm) as *H. africanum*, and both of these are figured as having short, 1-segmented exopods. The majority of the South African specimens have larger, 2-segmented exopods, while the exopods of those from Natal are smaller and 1-segmented. Jones (1956, 1960) mentioned the differences in size of some of the West African specimens, and the fact that those from South Africa are very large, but did not describe the exopods. In fact there is correlation between the size of the animals and the nature of the exopods. Those with 1-segmented exopods are smaller—Zimmer's largest was 4 mm, Kurian's 7–8 mm, and the Natal specimens reach 11,2 mm. Those with the bigger 2-segmented exopods are also larger in size—Fage's 16 mm, and the largest of the present specimens nearly 25 mm. The fact that 1-segmented exopods are present in adult animals from both India and Natal shows that this is not an age-dependent character, and it is therefore suggested that there are two distinct forms, insufficiently different to warrant specific rank. Those of Zimmer and Kurian, together with the NAD specimens are therefore designated *H. africanum africanum*, as opposed to those of Fage and Jones, and the majority of the specimens in the present collection, which become *H. africanum intermedium*.

Note: the size differences of the specimens identified by Jones (1956) in West Africa suggest that both forms may occur there.

Distribution of Heterocuma

H. sarsi, *H. armatum* and *H. andamani* are all shallow-water Indian Ocean or Indo-Pacific species. The two subspecies of *H. africanum* extend the range to the tropical Atlantic region.

Cumopsis G. O. Sars, 1878

Generic diagnosis

Vaunthompsoniinae with rudimentary exopods on pereiopods 2 and 3 in both sexes. Antenna 1 of male with a brush of sensory setae at base of flagellum. Basis of maxilliped produced distally very slightly or not at all, carpus not widened. Male with five pairs of pleopods. Telsonic somite truncate posteriorly, and not produced between the uropods. Endopod of uropod 2-segmented.
Type species *C. longipes* (A. Dohrn, 1869) as *Cuma longipes* from British Isles and Mediterranean.

KEY TO THE SPECIES OF *CUMOPSIS*

1 Dorso-lateral folds present..2
– Dorso-lateral folds absent..3

2 Two distinct lateral folds; carapace flattened dorsally................................ *C. goodsiri* (Van Beneden, 1861)—Europe, Indo-Pacific
– A single lateral fold; carapace convex dorsally.......*C. wafri* Jones, 1956—West Africa

3 Thoracic sideplates well defined dorsally..........*C. elongata* Jones, 1956—West Africa
– Thoracic sideplates not defined dorsally...4

4 Peduncle of uropod twice length of rami...5
– Peduncle of uropod only slightly longer than rami..................*C. robusta* sp. nov.

5 First segment of exopod of uropod longer than second............................. *C. fagei* Băcescu, 1956—W. France, Morocco
– First segment of exopod of uropod shorter than second............................. *C. longipes* (A. Dohrn, 1869)—Britain and Mediterranean

Cumopsis robusta sp. nov.

Figs 5 (♀), 6 (♂)

Records

LBT 5H	15.9.1970	32°04′S/18°18′E	3 m	Sand	1 ♀ ovig.	3,7 mm	HOLOTYPE
LBT 8L	15.9.1970	32°04′S/18°18′E	5 m	Sand	1 ♂ adult	4,0 mm	
LBT 105F	30.1.1972	32°04′S/18°18′E	LWS	Sand	5 ♀ ovig.	3,7–4,8 mm	
LBT 144A	Sept. 1972	32°04′S/18°18′E	LWS	Sand	2 ♀ ovig.	3,7–4,2 mm	
LBT 146E	Sept. 1972	32°04′S/18°18′E	1 m	Sand	1 ♂ subadult	3,6 mm	
LBT 147G	Sept. 1972	32°04′S/18°18′E	1 m	Sand	1 ♀	3,5 mm	
CP 833A	May 1972	False Bay (34°S/18°E)		Sand	1 ♀ ovig.	4,4 mm	
					1 ♀	3,2 mm	

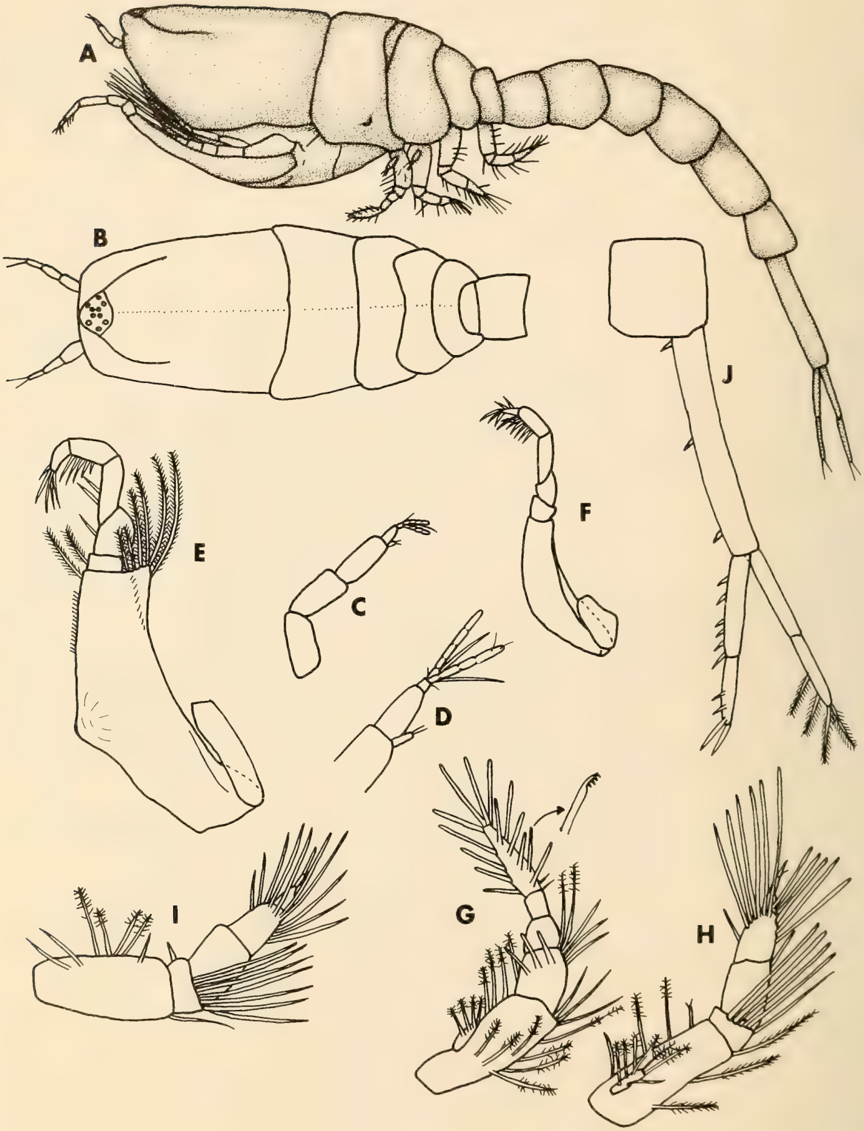

Fig. 5. *Cumopsis robusta* sp. nov.
Ovigerous female, holotype, 3,7 mm: A, lateral view; B, dorsal view of carapace; C, antenna 1; D, detail of distal end of antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, pereiopod 4; J, telsonic somite and uropod.

Holotype

Ovigerous female, deposited in the South African Museum, number SAM A13433.

Description

Ovigerous female, holotype, length 3,7 mm. Integument lightly calcified, with faint reticulations at high magnifications. Carapace nearly twice as long as deep, and equal in length to remaining free thoracic somites (Fig. 5A). No trace of lateral folds. Carapace in dorsal view (Fig. 5B) almost rectangular anteriorly due to short unproduced pseudorostral lobes being interrupted by eyelobe. Eye elliptical with a number of dark red pigmented rings; lenses not discernable. Antennal notch hardly defined. Cephalothorax just longer than abdomen. Abdominal somites without sideplates. Telsonic somite plus uropods equal in length to the four preceding somites. Mouthparts and lower edge of carapace dark in fresh specimens.

Three basal segments of antenna 1 (Fig. 5C) subequal, slight flexure between first and second. Flagellum with two aesthetascs. Accessory flagellum small, 1-segmented (Fig. 5D).

Basis of maxilliped 3 (Fig. 5E) half as long again as rest of limb, distally truncate, and broadly widened at its midpoint. Ischium half as long as wide. Merus slightly flared externally. Carpus and propodus subequal. Basal segment of exopod less than half length of basis.

Basis of pereiopod 1 (Fig. 5F) stout, just longer than remaining segments, of which carpus the longest. Basal segment of exopod $\frac{2}{5}$ length of basis, and slightly expanded at the mid-point.

Pereiopod 2 (Fig. 5G) stout. Ischium fused with basis. Carpus and propodus subequal. Dactyl equal in length to merus plus carpus, with many spines. Exopod 1-segmented, and about quarter length of basis, with four long plumose setae.

Pereiopod 3 (Fig. 5H) very stout. Basis equal in length to next four segments. Merus and carpus subequal. Exopod as in pereiopod 2.

Pereiopod 4 (Fig. 5I) stout, with many setae. No exopod.

Telsonic somite square in dorsal view (Fig. 5J), unarmed. Uropods equal in length to the four preceding somites. Peduncle just longer than rami, with three small spines on inner edge. First segment of endopod $1\frac{1}{2}$ times length of second, with six spines on inner edge; second segment with two spines on inner edge and two long terminal spines. Segments of exopod subequal, first unarmed, second with two plumose setae on inner edge and two long terminal ones.

Adult male, length 4,0 mm. Differs from female as follows: carapace $\frac{3}{4}$ as deep as long; cephalothorax equal in length to next five abdominal somites (Fig. 6A), which are more robust than in the female. Sideplates of pedigerous and abdominal somites defined ventrally, that of the fourth pedigerous somite being produced anteriorly. No antennal notch.

Antenna 1 (Figs 6B, 6C) very robust, with a brush of sensory setae surrounding the 2-segmented flagellum (Fig. 6D).

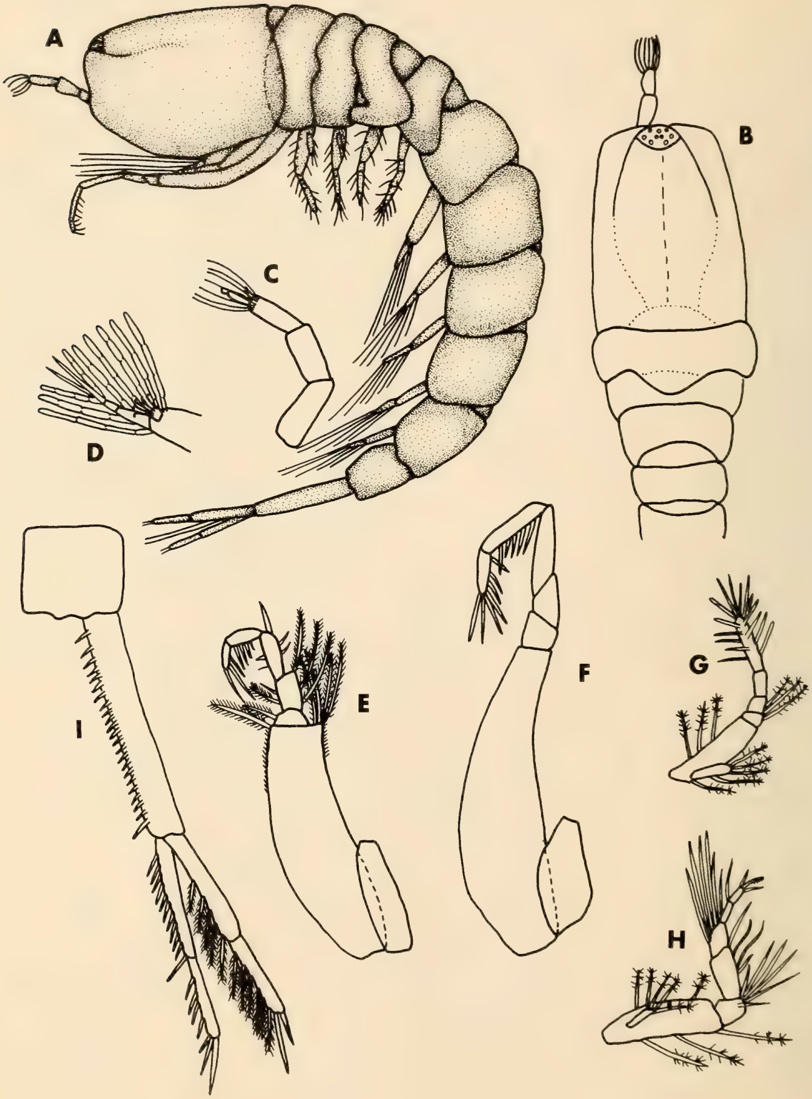

Fig. 6. *Cumopsis robusta* sp. nov.
Adult male, 4,0 mm: A, lateral view; B, dorsal view of carapace; C, antenna 1; D, detail of distal end of antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, telsonic somite and uropod.

Antenna 2 extending just beyond uropods—segments short.

Maxilliped 3 (Fig. 6E) with merus slightly expanded externally; less robust than in female, and basis not angled.

Propodus of pereiopod 1 (Fig. 6F) relatively shorter.

Pereiopods 2 and 3 (Figs 6G and 6H) less stout. Merus and carpus of pereiopod 2 shorter than propodus. Basal segment of exopod nearly half length of basis.

Telsonic somite and uropods (Fig. 6I) equal in length to the three preceding somites. Inner border of peduncle armed with about 23 small spines. Armature of rami greater than in female.

Remarks

The species of *Cumopsis* are rather similar morphologically. *C. robusta* may be distinguished from *C. fagei*, which it closely resembles, as follows: in *C. fagei* the peduncle of the uropods is almost twice the length of the endopod, while in *C. robusta* the two are almost subequal. In dorsal view the eyelobe and pseudorostral lobes form a straight line anteriorly in *C. robusta* while in *C. fagei* the pseudorostral lobes extend beyond the eyelobe for a short distance. The peduncle of the uropod is relatively broader and the rami are subequal in *C. robusta*, while the exopod is the longer in *C. fagei*.

Distribution of Cumopsis

This genus is found almost exclusively intertidally or in the infratidal fringe. It occurs in the British Isles, through the Mediterranean, tropical West Africa and South Africa to Annam. *C. robusta* would appear to be endemic to the south-western coast of South Africa.

Hypocuma Jones, 1973

Generic diagnosis

Vaunthompsoniinae with pseudorostral lobes produced anteriorly to meet in front of the eyeless eyelobe. No antennal notch or angle in either sex. Antenna 1 long and slender. Mandible normal. Five pairs of thoracic appendages bearing large flattened exopods in the male, and four in the female. Merus of maxillipeds 2 and 3 expanded, basis of maxilliped 3 not produced distally. Pereiopod 2 7-segmented. Well-developed exopods on first four pereiopods in male, and first three in female. Female with rudimentary exopod on pereiopod 4. Five pairs of pleopods in male. Telsonic somite produced between uropods. Type species *Hypocuma serratifrons* Jones, 1973 from 1 934 m off the Canary Islands.

Hypocuma dentatum sp. nov.

Figs 7 (♂), 8 (♀)

Records

SAM A10602a, *Pieter Faure* 17440: 34°25′S/17°50′E about 400 m
1 subadult ♂ 5,9 mm—uropods missing. HOLOTYPE
1 adult ♂ 6,0 mm—last somite missing
2 adult ♀—cephalothorax only

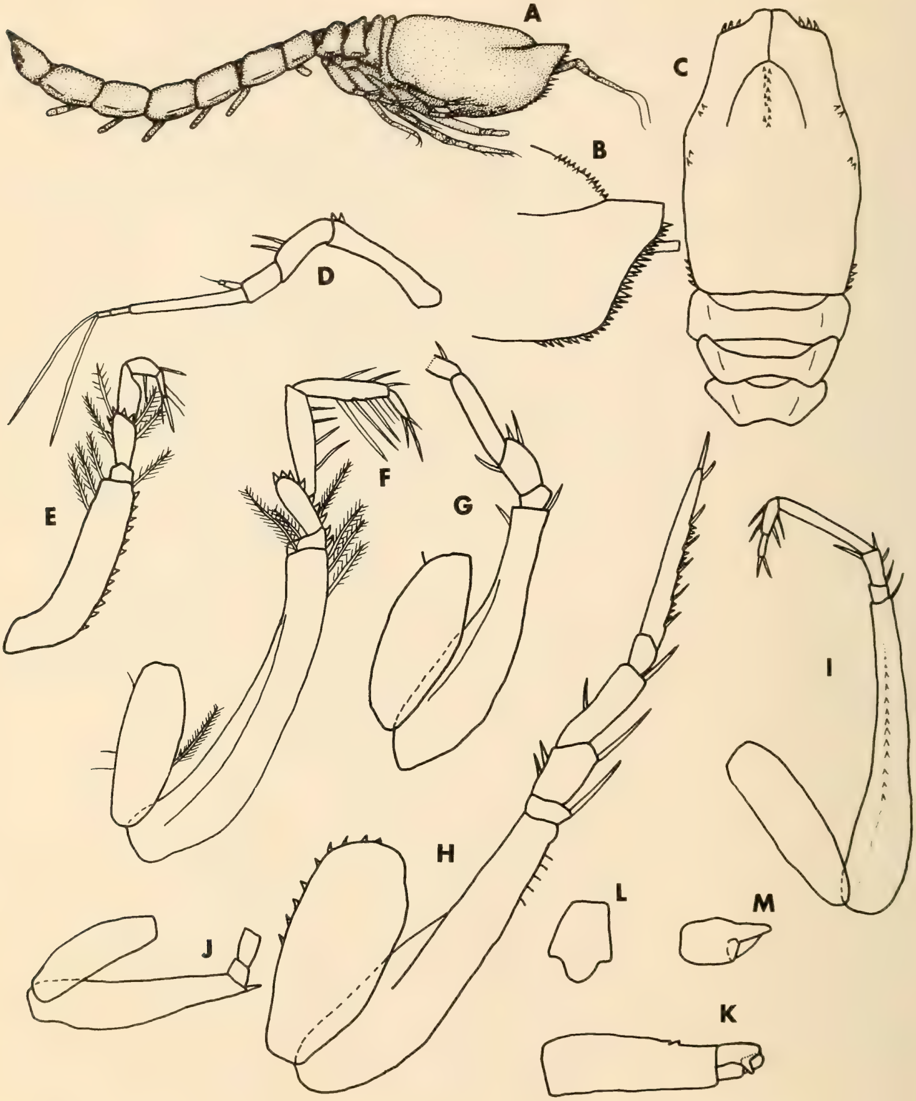

Fig. 7. *Hypocuma dentatum* sp. nov.
Adult male, holotype, 5,9 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, antenna 1; E, maxilliped 2; F, maxilliped 3; G, pereiopod 1; H, pereiopod 2; I, pereiopod 3; J, pereiopod 4; K, pleopod 2; L, dorsal view of telsonic somite; M, lateral view of telsonic somite.

Holotype

Subadult male, deposited in the South African Museum, number SAM A13434.

Description

Subadult male, holotype, length 5,9 mm. Carapace twice as long as deep with slightly upturned pseudorostrum reaching well beyond eyelobe and constituting $\frac{1}{5}$ total length of carapace (Fig. 7A). No antennal notch (Fig. 7B). A row of well-developed denticles on anterior edges of carapace, becoming smaller and disappearing along ventral edge. Eyelobe eyeless with a row of small denticles dorsally (Fig. 7C). Exoskeleton generally sculptured with triangular denticles of varying size. Carapace $1\frac{1}{2}$ times length of free thoracic somites, and of almost equal length to first four abdominal somites. First pedigerous somite visible dorsally and laterally, second to fourth with slight ventro-lateral flanging. Abdominal somites with well-developed sideplates. Telsonic somite produced between uropods for about $\frac{1}{3}$ its length.

Antenna 1 (Fig. 7D) slender, elongate, and geniculate between first and second segments. Flagellum 3-segmented, with first segment greatly elongated. Accessory flagellum small, 2-segmented.

Maxilliped 2 (Fig. 7E) with a row of denticles on inner edge of basis; ischium small; merus and carpus subequal, inner edge of merus expanded distally, and bearing five denticles.

Maxilliped 3 (Fig. 7F) with basis slightly longer than combined length of remaining segments, and not produced distally. Ischium twice as wide as long, with two denticles on inner edge. Merus expanded externally with seven denticles along inner and distal edges. Carpus and propodus subequal, and each $1\frac{1}{2}$ times length of merus. Dactyl small. Basal segment of exopod oval, and less than half length of basis.

Pereiopod 1 (Fig. 7G) relatively short. Ischium as broad as long, and slightly expanded internally, as is the merus. Merus twice length of ischium. Carpus cylindrical, twice length of merus. Dactyl and part of propodus missing. Exopod very well developed, basal segment $\frac{2}{3}$ length of basis.

Pereiopod 2 (Fig. 7H) largest of the legs, nearly $2\frac{1}{2}$ times length of basis of pereiopod 1. Basis slightly keeled to accommodate the large exopod, which has basal segment $\frac{3}{4}$ length of basis, flattened, with a row of 9–10 denticles along the outer and distal edges. Ischium half as long as broad. Merus three times length of ischium. Carpus cylindrical, equal in length to ischium plus merus. Propodus small, just more than $\frac{1}{3}$ length of carpus. Dactyl elongate, equal in length to ischium, merus and carpus together, with a small terminal spine and five lateral spines on inner edge, interspersed with small denticles.

Pereiopod 3 (Fig. 7I) smaller, reaching end of carpus of pereiopod 2. Basal segment of exopod smaller and less expanded, slightly more than half length of basis. Basis long and straight, $1\frac{1}{2}$ times length of rest of limb, with a row of denticles along its length. Ischium square, merus twice its length. Carpus

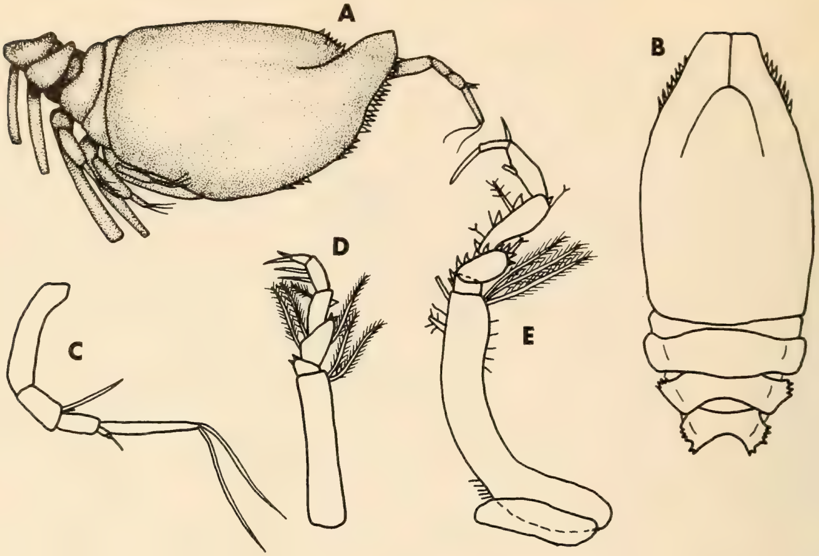

Fig. 8. *Hypocuma dentatum* sp. nov.
Adult female, paratype, carapace length 2,0 mm: A, lateral view of cephalothorax; B, dorsal view of cephalothorax; C, antenna 1; D, maxilliped 2; E, maxilliped 3.

elongate, twice length of ischium plus merus. Propodus and dactyl small, subequal.

Pereiopod 4 (Fig. 7J) smaller still, with basal segment of exopod $\frac{2}{3}$ length of basis. Ischium square, merus slightly longer. Rest of limb missing. Pereiopod 5 missing.

Five pairs of pleopods (Fig. 7K), each with a sharp external projection on inner ramus.

Telsonic somite (Figs 7L, 7M) produced between insertion of uropods for $\frac{1}{3}$ its length, unarmed. Uropods missing.

Adult female, paratype, length of carapace 2,0 mm. Last thoracic segment and abdomen missing in both specimens. Only bases of pereiopods retained.

Carapace similar to male, but deeper, about $1\frac{1}{2}$ times as long as deep (Fig. 8A), with denticles on anterior edge. Pseudorostrum just less than a quarter length of carapace, and more upturned than in male. No eye (Fig. 8B).

Antenna 1 (Fig. 8C) less elongate. First segment longest, second and third subequal and together about $\frac{3}{4}$ length of first. Accessory flagellum with minute second segment. Flagellum 1-segmented, and nearly as long as basal segment.

Maxilliped 2 (Fig. 8D) with merus more expanded internally than in male.

Maxilliped 3 (Fig. 8E) with exopod $\frac{2}{5}$ length of basis. Merus expanded internally, but not as elongated as in male.

Pereiopods represented by bases only, that of pereiopod 2 largest. Articulation of exopod of pereiopod 3 visible, but exopod missing.

Remarks

H. dentatum quite obviously belongs to the genus *Hypocuma*, and the differences between it and *H. serratifrons* are not great. The two species may be distinguished as follows: in *H. dentatum* the exoskeleton is covered by scattered denticles of varying size, those on the anterior edge of the carapace being particularly distinctive, and larger than in *H. serratifrons*. The general shape of the carapace differs, mainly in the lack of a depression behind the pseudorostrum in *H. dentatum* and the nature and degree of tilting of the pseudorostral lobes. The telsonic somite protrudes between the uropods for less than $\frac{1}{3}$ its length in *H. dentatum*, and for nearly half in *H. serratifrons*. The flagellum of the first antenna in *H. serratifrons* is 2-segmented in both the male and the female, and in *H. dentatum* is apparently 1-segmented in the female, and 3-segmented in the male, but since the specimens of *H. dentatum* are very old and quite decalcified, it is difficult to be certain about the exact position of some sutures.

Distribution of Hypocuma

The single sample of *H. dentatum* was obtained from about 400 m off Cape Point. No substrate data are given. The very considerable development of the exopods of the male thoracic appendages indicates that it is an active swimmer. Further collecting off the south and east coasts of southern Africa is needed to determine the distribution range. *H. serratifrons* Jones is also represented by a single sample, from 1 934 m off the Canary Islands.

Vaunthompsonia Bate, 1858

Generic diagnosis

Pseudorostrum short, eyes present. All pedigerous somites visible from above. Telsonic somite slightly produced between uropods. Antenna 1 short with 1-segmented accessory flagellum. Basis of maxilliped 3 not produced distally. Exopods present on pereiopods 1–4 in male and 1–3 in female. Male with five pairs of pleopods. Endopod of uropod 2-segmented.
Type species *Vaunthompsonia cristata* (Bate, 1856), British Isles, Mediterranean, West Indies, Indo-Pacific, South Africa.

KEY TO THE SPECIES OF *VAUNTHOMPSONIA*

1 Peduncle of uropods longer than telsonic somite....................................2
– Peduncle of uropods shorter than or equal to telsonic somite..........................3

2 Pereiopod 1 reaching end of carapace with part of propodus; dorsal outline not strongly arched .... *V. cristata* (Bate, 1856)—widespread
– Pereiopod 1 reaching end of carapace with dactyl only; dorsal outline strongly arched.... *V. arabica* Calman, 1907—India

3 Antero-lateral borders of carapace serrated...4
– Antero-lateral borders of carapace not serrated.....................................6

4 Minute serrations on antero-lateral border only................. *V.* sp.—South Africa
– Serrations present on carapace apart from antero-lateral border.......................5

5 Single row of mid-dorsal serrations on carapace...... *V. serratifrons* Gamô, 1964—Japan
– A double row of serrations on posterior half of carapace, converging towards posterior border .... *V. meridionalis* G. O. Sars, 1887—Antarctica

6 Basis of maxilliped 3 somewhat produced distally... *V. inermis* Zimmer, 1909—Antarctica
– Basis of maxilliped 3 not produced 7
7 Length of telsonic somite anterior to insertion of peduncle greater than length posterior to insertion 8
– Length of telsonic somite anterior to insertion of peduncle shorter than or equal to length posterior to insertion...9

8 First segment of exopod almost equal in length to second of endopod.................. *V. natalensis* sp. nov.—South Africa
– First segment of exopod half length of second segment of endopod................... *V. media* Zimmer, 1952—Indochina

9 Pereiopod 1 with basal segment of exopod $\frac{2}{3}$ length of basis; first two segments of antenna 1 longer than rest of appendage 10
– Pereiopod 1 with basal segment of exopod $\frac{2}{5}$ length of basis; first two segments of antenna 1 shorter than rest of appendage................. *V. dawydoffi* Zimmer, 1952—Indochina

10 First segment of exopod of uropod $\frac{1}{6}$ length of second.............................. *V. floridana* Băcescu, 1971—Caribbean
– First segment of exopod of uropod $\frac{1}{2}$ length of second .... *V. nana* Hale, 1944—Australia

Vaunthompsonia cristata (Bate, 1856)

Vaunthompsonia cristata: G. O. Sars, 1879: 22, pl. 23–26, figs 17–18. Stebbing, 1913: 10, figs 5–7.

Records

One specimen from False Bay (34°S/18°E), depth 5 m

Holotype

Designated by Bate, 1856, from western France. ?British Museum (Natural History).

Remarks

This species, represented by a single damaged male, was identified by Jones (1960) from UCT material taken from False Bay. Dr Jones has kindly re-examined the material, which is still in his possession, and confirms his original identification.

Distribution

Widespread—British Isles, Mediterranean, Annam, Japan, West Indies, South Africa, in shallow waters.

Vaunthompsonia natalensis sp. nov.

Figs 9 (♀), 10 (♂)

Records

SCD 272 Y	19.7.1961	34°23′S/25°54′E	Sand and shell	182 m	1 ♀ ovig.	3,4 mm
SCD 321 L	9.7.1962	34°15′S/25°50′E	Fine sand	108 m	1 subadult ♂	3,0 mm
Coast 4/P3	6.2.1973	30°37′S/30°40′E		75 m	1 ♀	2,0 mm
Coast 4/Q2	6.2.1973	30°46′S/30°31′E		48 m	1 ♀	1,8 mm

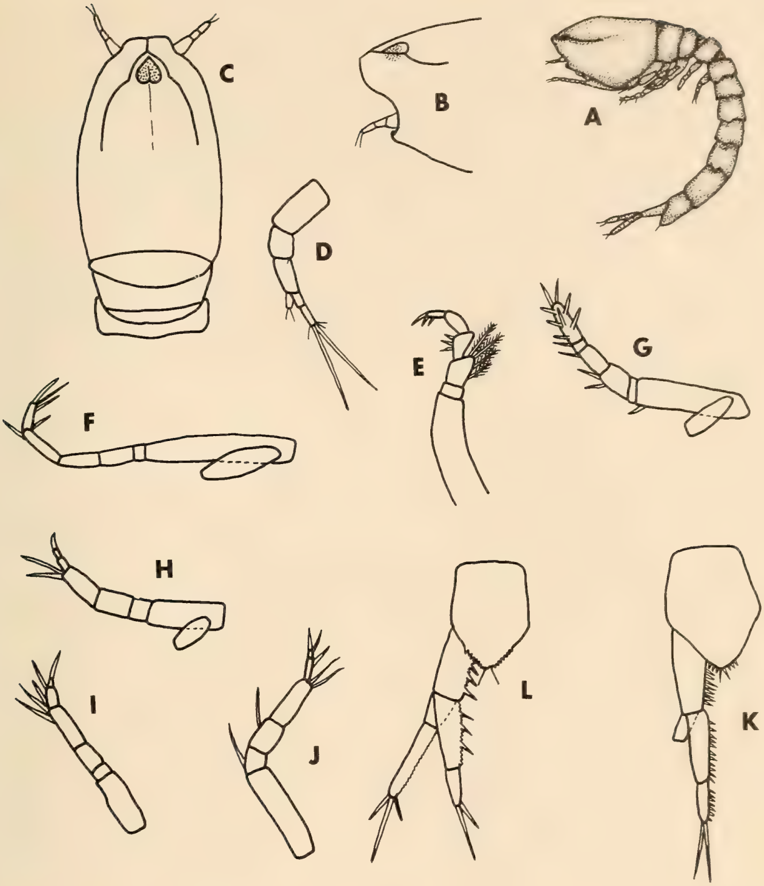

Fig. 9. *Vaunthompsonia natalensis* sp. nov.
Adult female, holotype, 3,4 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, pereiopod 4; J, pereiopod 5; K, telsonic somite and uropod of adult; L, telsonic somite and uropod of juvenile.

Holotype

Ovigerous female deposited in the South African Museum, number SAM A13435.

Description

Ovigerous female, holotype, length 3,4 mm. Body compact, smooth, without serrations (Fig. 9A). Carapace about $\frac{2}{3}$ as deep as long, somewhat vaulted anteriorly with faint mid-dorsal carina on eyelobe. Antennal notch shallow, antero-lateral angle defined by a small tooth (Fig. 9B). Eye obvious, heart-shaped in dorsal view, with no visible lenses (Fig. 9C). Pseudorostrum meeting in front of the rounded eyelobe for a short distance. Carapace a quarter as long again as free thoracic somites, all of which are visible dorsally. Cephalothorax as long as abdomen excluding uropods. Abdominal somites cylindrical, each with a small posterior articulatory process. Telsonic somite produced between uropods for half its length, with several fine spines between uropods, and two fine anal setae (minutely serrated between uropods in juveniles).

Antenna 1 (Fig. 9D) with basal segment longest, and second segment shortest. Flagellum 2-segmented with two terminal setae. Accessory flagellum 1-segmented.

Basal segment of maxilliped 3 (Fig. 9E) not produced. Ischium twice as broad as long. Merus somewhat expanded distally, and slightly longer than broad. Carpus widened distally, subequal to merus. Propodus and dactyl nearly subequal.

Pereiopod 1 (Fig. 9F) fairly elongate, with dactyl and part of propodus extending beyond carapace anteriorly. Basis equal in length to next four segments. Ischium small, square. Next four segments almost subequal. Basal segment of exopod half length of basis.

Pereiopod 2 (Fig. 9G) relatively stout, 7-segmented. Ischium $\frac{1}{3}$ as long as wide, merus and carpus subequal. Propodus $\frac{1}{3}$ length of dactyl, which bears a number of spines. Basal segment of exopod less than half length of basis.

Pereiopods 3–5 (Figs 9H–J) similar, except for exopod of pereiopod 3. Basis of pereiopod 5 longest.

Peduncle of uropod stout, shorter than telsonic somite (Fig. 9K) with seven sharp setae on inner edge; juveniles with three spines on minutely serrated inner edge (Fig. 9L). Rami of juveniles subequal. First segment of endopod of adult twice length of second with ten small spines on inner edge; juveniles with three spines on serrated inner edge. Second segment of adult with six small spines on inner edge (juveniles unarmed) and two terminal spines in all three specimens. Exopod of juveniles with first segment $\frac{2}{5}$ length of second, unarmed. Second segment missing in holotype; minutely serrated on inner edge of juveniles, with two short spines and one terminally.

Subadult male length 3,0 mm. Differs from the female as follows: generally more robust; carapace slightly less deep (Fig. 10A). Eye with a ring of 11 lenses around edge of pigmented area (Fig. 10B).

First segment of flagellum of antenna 1 longer than second (Fig. 10C).

Merus of maxilliped 3 (Fig. 10E) slightly longer and broader. Carpus not expanded.

Last five segments of pereiopod 1 missing.

Five pairs of pleopods present (Fig. 10H).

Shape of telsonic somite as in female, but unserrated posteriorly (Fig. 10I). Peduncle of uropod slightly longer, with nine spines on inner edge. First segment of exopod unarmed, half length of second; second bearing four small spines on outer and three on inner edge, and three terminally. First segment of endopod twice length of second, with 12 sharp spines on inner edge; second with five small spines on inner edge, and three terminally.

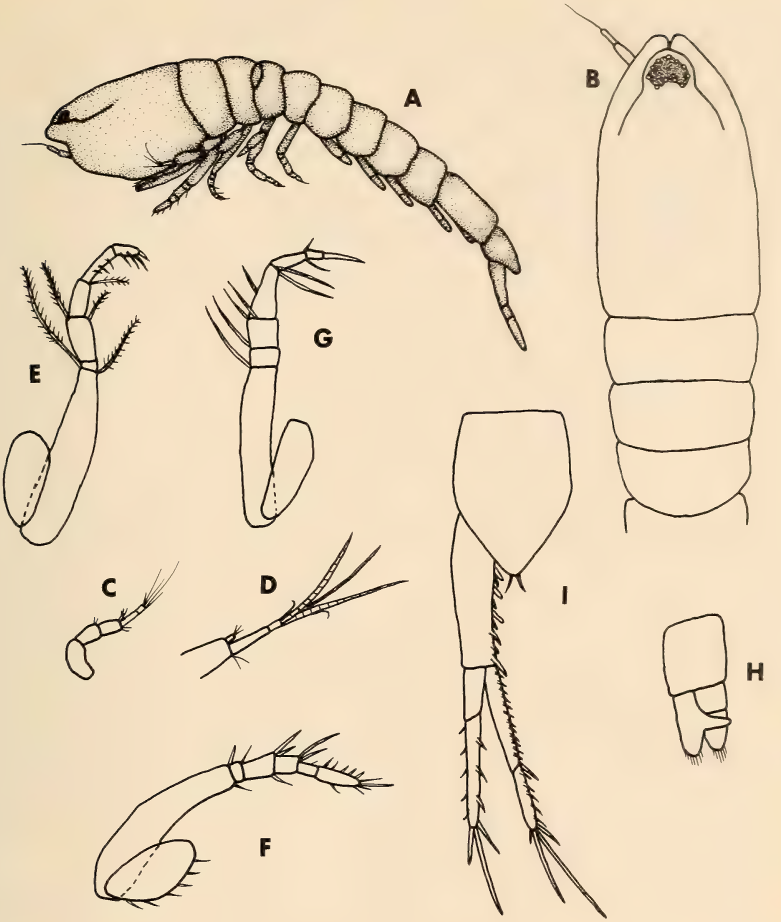

Fig. 10. *Vaunthompsonia natalensis* sp. nov.
Subadult male, 3,0 mm: A, lateral view; B, dorsal view of carapace; C, antenna 1; D, detail of distal end of antenna 1; E, maxilliped 3; F, pereiopod 2; G, pereiopod 4; H, pleopod 3; I, telsonic somite and uropod.

Remarks

This species conforms to the general facies of the genus. It differs from the other unserrated members as follows: the carapace of the female is somewhat deepened midway along its length; the eye is heart-shaped in dorsal view; the merus of maxilliped 3 is slightly broadened distally, particularly in the female. The exopods of the pereiopods are smaller and narrower than those of other species, and the peduncles and rami of the uropods are particularly stout. The proportions of the uropodal segments are distinctive, especially in that the first segment of the exopod and the second of the endopod are subequal.

Distribution

Endemic to Natal from 45 to 182 m.

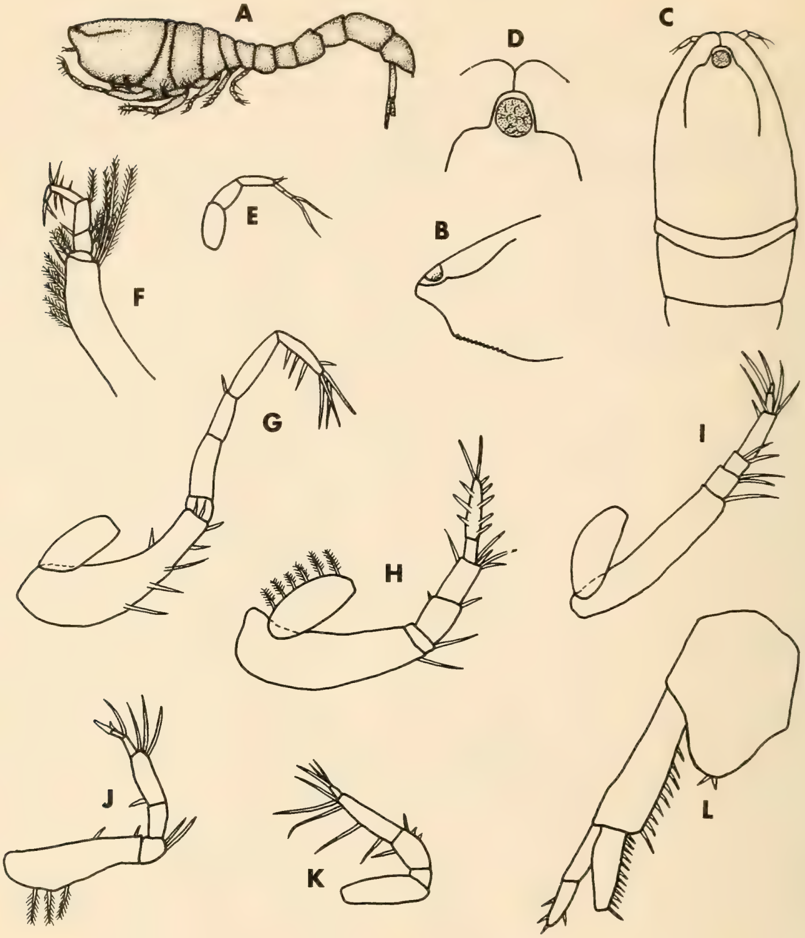

Fig. 11. *Vaunthompsonia* sp.
Adult female, 4,4 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, detail of anterior end of carapace in dorsal view; E, antenna 1; F, maxilliped 3; G, pereiopod 1; H, pereiopod 2; I, pereiopod 3; J, pereiopod 4; K, pereiopod 5; L, telsonic somite and uropod.

Vaunthompsonia sp.

Fig. 11

Records

WCD 95 V	3.7.1961	33°06′S/17°49′E	88 m	Mud and rock	1 ♀	4,4 mm

Description

Adult female, length 4,4 mm. In most respects (Figs 11A–D, F, H–K) similar to *V. media* Zimmer, 1952, from Annam, but differs in the length of the basal segment of antenna 1 (Fig. 11E), in the relative lengths of the merus and carpus of pereiopod 1 (Fig. 11G) and the telsonic somite and uropods (Fig. 11L), described below.

Telsonic somite $\frac{3}{4}$ as wide as long at its widest point, and produced between uropods for half its length, terminating in two small anal setae. Ratio of outer edge of telsonic somite: outer edge of peduncle is 1 : 2. Peduncle with nine spines on inner edge. First segment of endopod slightly more than half length of peduncle, with 12 fine spinules along inner edge. Second segment missing. First segment of exopod $\frac{3}{4}$ as long as first segment of endopod, unarmed. Second segment just shorter than first, with four small spines near the end.

Remarks

Since neither of the uropods of the single female is complete, and since Zimmer described *V. media* on the basis of adult males, certain identification or the erection of a new species should await further material. The specimen differs from *V. natalensis* in the shape of the carapace, in the basis and carpus of maxilliped 3, in the presence of serrations on the lower border of the carapace and in particular in the proportions of the telsonic somite, and the peduncle and rami of the uropods.

Distribution of Vaunthompsonia

Vaunthompsonia has the widest distribution of any of the genera under consideration. Species occur from the British Isles (*V. cristata*) to South Georgia and Kerguelen (*V. meridionalis* and *V. inermis*), Japan (*V. serratifrons*) and Australia (*V. nana*). The genus is generally confined to waters shallower than 250 m, but *V. meridionalis* has been found at 315 m in South Georgia.

Bathycuma Hansen, 1895

Generic diagnosis

Pseudorostral lobes meeting anteriorly. Eye absent. First pedigerous somite exposed. Telsonic somite produced between uropods. Basis of maxilliped 3 produced distally. Exopods present on pereiopods 1–4 in male, and 1–3 in female. Male with five pairs of pleopods. Endopod of uropod 2-segmented.
Type species *B. elongatum* Hansen, 1895, from 4 980 m in the central Atlantic.

KEY TO THE SPECIES OF *BATHYCUMA*

1 Lateral carinae on pleon somites 2
– Pleon somites not carinate 3

2 Distal prolongation of basis of maxilliped 3 not reaching end of merus ....
B. longicaudatum Calman, 1912 – California
– Distal prolongation of basis of maxilliped 3 reaching beyond end of merus ....
B. magnum Jones, 1969 – Indian Ocean

3 Pereiopod 2 with six segments .... *B. elongatum* Hansen, 1895 – Atlantic
– Pereiopod 2 with seven segments 4

4 Segments of endopod of uropod not subequal..5
– Segments of subequal endopod of uropod..6

5 First segment of endopod of uropod twice length of second; prolongation of basis of maxilliped 3 reaching middle of merus........*B. capense* (Zimmer, 1921)—South Africa
– First segment of endopod of uropod shorter than second; prolongation of basis of maxilliped 3 reaching end of merus......................*B. brevirostre* (Norman, 1879)—Europe

6 Carapace without mid-dorsal serrations; segments of exopod of uropod subequal........ *B. datum* sp. nov.—South Africa
– Carapace with mid-dorsal serrations; first segment of exopod of uropod half length of second 7

7 Uropods more than twice length of telsonic somite; first segment of endopod distinctly longer than second........................*B. natalense* Stebbing, 1912—South Africa
– Uropods less than half length of telsonic somite; first segment of endopod just longer than second .... *B. longirostre* Calman, 1905—Malaya

Bathycuma capense (Zimmer, 1921)

Figs 12 (♀), 13A–D (♂)

Vaunthompsonia capensis Zimmer, 1921: 131, figs 28–29.

Records

SAM A10602c, *Pieter Faure* 17440:		34°20′S/18°50′E	about 400 m		1 ♂ 7,2 mm
WCD 77 A	8.10.1960	34°17′S/17°53′E	320 m	Sand and mud	1 ♀ adult 10,9 mm 1 ♂ subadult 10,2 mm
SCD 405 E	?	34°10′S/20°12′E	about 200 m	Sand	4 ♀ 8,6–10,2 mm 2 ♂ subadult 9,9–10,2 mm 1 juv. 4,6 mm

Holotype designated by Zimmer (1921) from Agulhas Bank 35°19′S/20°12′E 140 m. Zoologisches Museum, Berlin.

Description

Adult female, length 10,2 mm. Body elongate, carapace short, vaulted, a little more than $1\frac{1}{2}$ times as long as deep (Fig. 12A), mid-dorsal carina bearing numerous small teeth anteriorly. Pseudorostral lobes meeting in front of very small eyeless eyelobe for $\frac{1}{10}$ length of carapace (Fig. 12C). Antennal notch not deep, but dorso-ventrally excavated with several minute teeth above (Fig. 12B). Antero-lateral angle acute, defined by a large tooth with several small serrations along the ventro-lateral margin. Carapace just longer than rest of thorax. Pedigerous somites all exposed, second, third and fourth with slight flanges visible dorsally. Cephalothorax just shorter than next five abdominal somites which are cylindrical in cross-section. Telsonic somite produced between uropods for $\frac{1}{3}$ its length.

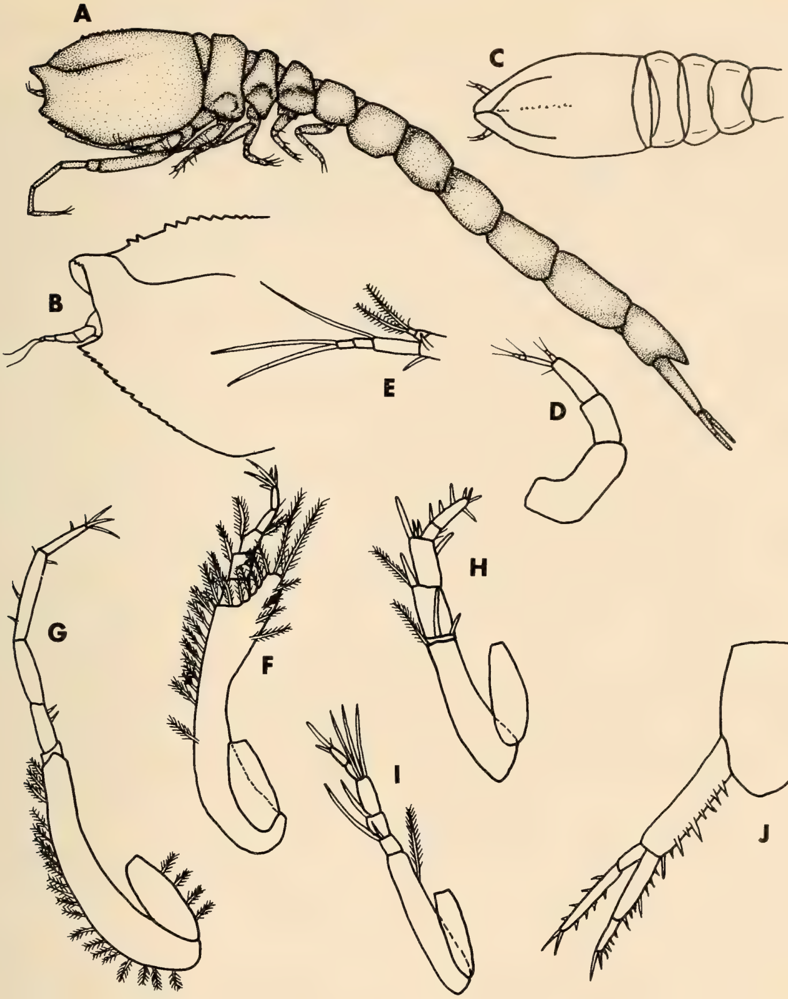

Fig. 12. *Bathycuma capense* (Zimmer, 1921)
Adult female, 10,2 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, antenna 1; E, detail of distal end of antenna 1; F, maxilliped 3; G, pereiopod 1; H, pereiopod 2; I, pereiopod 3; J, telsonic somite and uropod.

Antenna 1 (Fig. 12D) robust, first segment geniculate and longer than next two together. Second segment just shorter than third. Flagellum (Fig. 12E) 3-segmented, nearly as long as second basal segment, with two terminal setae. 2-segmented accessory flagellum half as long as first of flagellar segments, with two plumose terminal setae.

Maxilliped 3 (Fig. 12F) setiferous. Basis more than twice length of remaining segments, with a distal prolongation reaching half way along merus. Other segments subequal, ischium slightly longest and stoutest. Basal segment of exopod more than quarter length of basis.

Pereiopod 1 (Fig. 12G) elongate, with propodus and dactyl exceeding tip of pseudorostrum. Basis setiferous. Ischium broader than long. Carpus equal to ischium plus merus. Propodus and dactyl long and slender. Basal segment of exopod $\frac{2}{5}$ length of basis.

Pereiopod 2 (Fig. 12H) fairly stout, basis nearly as long as last four segments. Ischium distinct but very short. Merus and carpus subequal, stout, each with a strong distal spine. Propodus $\frac{1}{3}$ length of merus. Dactyl relatively short, twice length of propodus, with a few small spines. Basal segment of exopod $\frac{2}{3}$ length of basis.

Pereiopod 3 (Fig. 12I) more slender. Basis longer than remaining segments together, of which carpus is longest. Exopod as in pereiopod 2.

Peduncle of uropods shorter than telsonic somite (Fig. 12J) with nine uneven spines along inner edge. Exopod just longer than endopod and just shorter than peduncle. First segment of exopod less than half length of second, unarmed. Second segment with four small spines on both edges, and two terminally. First segment of endopod more than twice length of second, with seven small spines on inner edge. Second segment with four spines on inner edge and two terminally.

Subadult male, length 10,2 mm. As in female, except: carapace more rectangular in outline; pseudorostral lobes $\frac{1}{7}$ total length of carapace (Fig. 13A). Antennal notch much shallower, angle obtuse with finer teeth below (Fig. 13B). Length of cephalothorax somewhat less than length of next five abdominal somites.

Antenna 1 (Fig. 13C) with first segment not geniculate, accessory flagellum longer, flagellum 2-segmented, terminating in two aesthetascs.

Thoracic appendages as in female, but pereiopod 1 longer, with carpus exceeding tip of pseudorostrum.

Armature of uropods more extensive (Fig. 13D).

Remarks

Zimmer (1921) described *B. capense* as *Vaunthompsonia capensis* from a single subadult male, figuring only the entire animal and a uropod. Although he did not accept the genus *Bathycuma*, considering it at most to be a subgenus of *Vaunthompsonia*, it is quite obvious that Zimmer's specimen belongs to *Bathycuma* as now accepted. I am unable to find any significant differences between Zimmer's description and the present material.

Bathycuma natalense Stebbing, 1912

Figs 13E–J (♂), 14 (♀)

Bathycuma natalense Stebbing, 1912: 135, pl. 49.

Records

SST 66 C	21.7.1972	34°23′S/21°26′E	15 m	Sand and shell	1 ♀ adult	9,0 mm
					1 ♀	6,5 mm
					1 ♂	6,1 mm

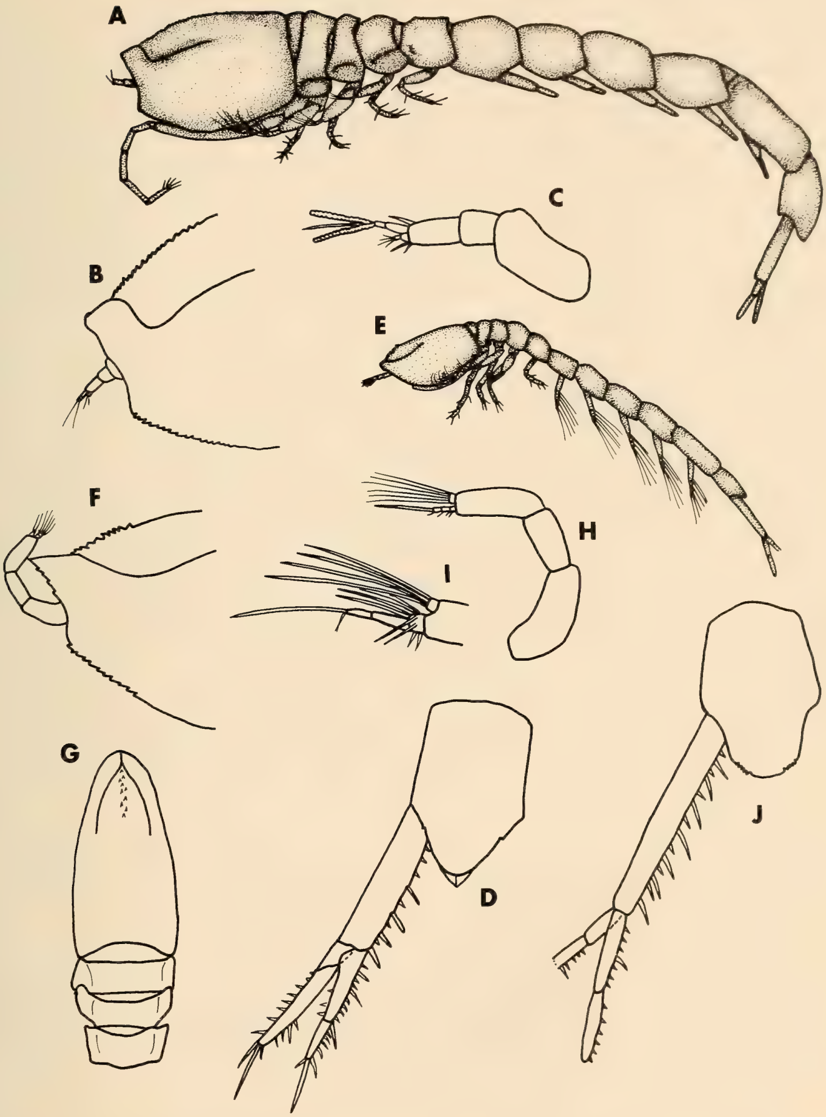

Fig. 13. *Bathycuma capense* (Zimmer, 1921)
Subadult male, 10,2 mm: A, lateral view; B, anterior end of carapace; C, antenna 1; D, telsonic somite and uropod.
Bathycuma natalense Stebbing, 1912
Adult male, 11,2 mm: E, lateral view; F, detail of anterior end of carapace; G, dorsal view of carapace; H, antenna 1; I, detail of distal segments of antenna 1; J, telsonic somite and uropod.

Holotype designated by Stebbing (1912): *Pieter Faure* 12605, 30°10′S/31°03′E 410 m, 2 adult males. British Museum (Natural History).

Description

Adult female, length 9,0 mm. Carapace elongate, less than twice as long as broad, serrated mid-dorsally along eyelobe (Fig. 14A). Pseudorostrum relatively long, meeting in front of small triangular eyelobe for $\frac{1}{6}$ of total length of carapace (Fig. 14E). Antennal notch (Fig. 14B) semicircular, fairly small but well-defined by a large antero-lateral tooth with a few serrations running along ventro-lateral border. Carapace longer than free thoracic somites which are slightly flanged laterally. Cephalothorax just longer than next five abdominal somites, which are cylindrical in cross-section and lack carinae. Telsonic somite produced between uropods for nearly $\frac{1}{3}$ its length.

Antenna 1 (Fig. 14C) fairly long and slender. Basal segment geniculate, next two subequal, each $\frac{2}{3}$ length of basal segment. Flagellum (Fig. 14D) 2-segmented, first twice length of second, which bears two aesthetascs. Accessory flagellum 2-segmented and $\frac{2}{3}$ length of first flagellar segment.

Maxilliped 3 (Figs 14F and 14G) with basis three times length of remaining segments. Distal prolongation almost reaching end of merus, with four small denticles on inner edge just below insertion of ischium. Ischium just longer than wide with single denticle on inner distal edge. Merus slightly longer than ischium, somewhat expanded externally with two denticles at apex of expansion. Carpus and merus subequal, propodus and dactyl subequal, shorter than carpus. Basal segment of exopod less than $\frac{1}{3}$ length of basis.

Basis of pereiopod 1 (Fig. 14H) long and slender. Ischium short with a single spine on slightly expanded inner edge. Merus twice length of ischium. Carpus and rest of limb missing in this and all other specimens. Basal segment of exopod $\frac{1}{3}$ length of basis.

Basis of pereiopod 2 (Fig. 14I) equal in length to last four segments. Ischium as long as broad, merus $2\frac{1}{2}$ times length of ischium. Carpus equal to ischium plus merus. Dactyl fairly stout and equal in length to carpus. Basal segment of exopod more than half length of basis.

Basis of pereiopod 3 (Fig. 14J) longer than rest of leg. Ischium slightly broader than long, merus $1\frac{1}{2}$ times length of ischium. Carpus longer than ischium and merus together, and twice length of propodus and dactyl together. Basal segment of exopod $\frac{2}{3}$ length of basis.

Pereiopods 4 and 5 without exopods.

Peduncle of uropod longer than telsonic somite (Fig. 14K), with about 13 spines arranged in two rows along inner edge. Exopod $\frac{2}{3}$ length of peduncle, first segment unarmed, half length of second, which has eight small spines on outer and five on inner edge, and three terminally. First segment of endopod slightly longer than first segment of exopod, with four spines on inner edge. Second segment missing.

Adult male, length 11,2 mm. As the male is in poor condition, Stebbing's

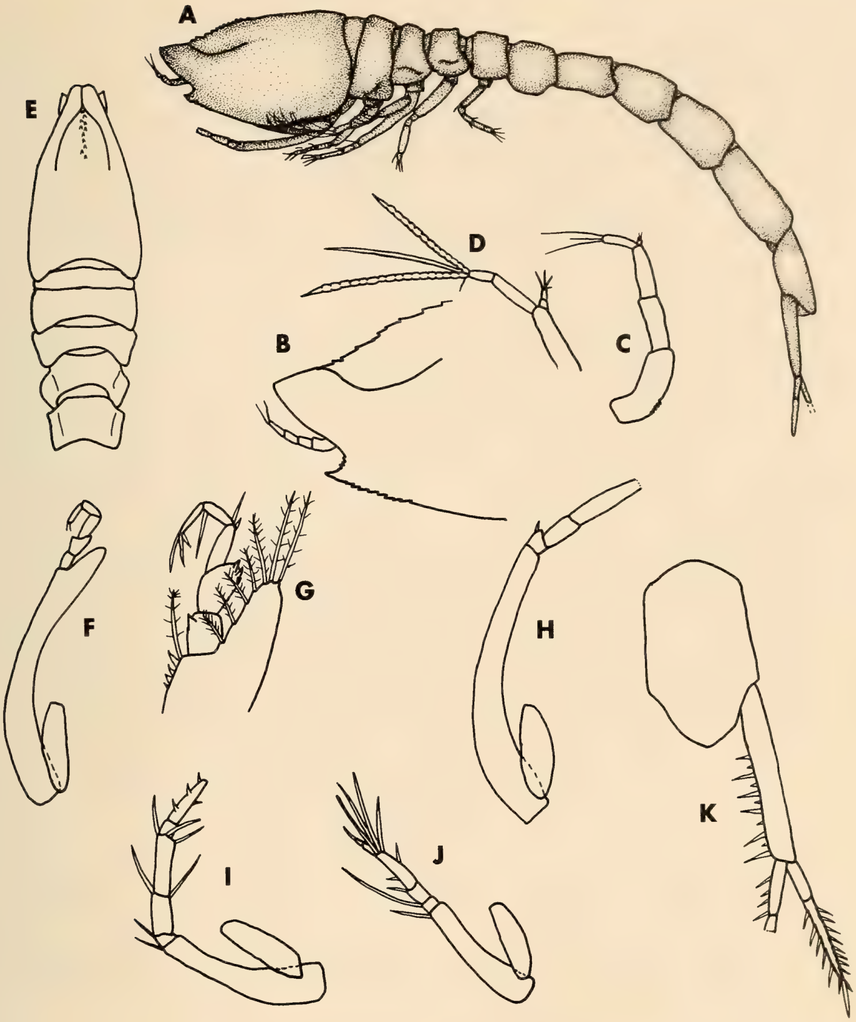

Fig. 14. *Bathycuma natalense* Stebbing, 1912.
Adult female, 9,0 mm: A, lateral view; B, detail of anterior end of carapace; C, antenna 1; D, detail of distal end of antenna 1; E, dorsal view of carapace; F, maxilliped 3; G, distal segments of maxilliped 3; H, pereiopod 1; I, pereiopod 2; J, pereiopod 3; K, telsonic somite and uropod.

type is redescribed where it differs from the female. The whole animal (Figs 13E and G) is refigured, as the type specimens do not correspond well with his original figures.

Carapace as in female, but lacking antennal notch and antero-lateral angle (Fig. 13E). Twice as long as deep, and more vaulted anteriorly with serrations on ventral edge of pseudorostral lobes.

Antenna 1 (Fig. 13H) unusual, extremely robust, with numerous setae on the accessory flagellum (Fig. 13I). Basal segment geniculate. Flagellum 3-segmented, first segment small with a number of setae; second twice length of first, third just longer than first with a single terminal spine. Accessory flagellum 1-segmented with numerous long setae.

Pereiopods as in female.

Telsonic somite (Fig. 13K) with minute serrations laterally, posterior to insertion of uropods. Uropods and first segment of endopod relatively longer.

Remarks

In most respects, this species is similar to other members of the genus, but is distinguished by the greater length of the peduncle of the uropods, and the very robust first antennae of the male. *B. natalense* and *B. capense* are similar to each other in general appearance, and are probably closely related. In addition to the differences in the first antennae of the adult males, however, they are also distinguished by the relative lengths of the uropods and the different shapes of the carapace.

The depth of the type specimen (about 400 m) is fairly typical for the genus, but the shallow depth of 15 m for the SST sample seems inexplicable. Records, logs and labels have been checked and seem to be correct. The greatest depth reached in this particular transect was 200 m, so that even had a labelling error occurred, the depth is surprisingly shallow. Further collecting is required to determine whether in fact *B. natalense* does normally occur at such shallow depths.

Bathycuma datum sp. nov.

Fig. 15

Records

SAM A10602b, *Pieter Faure* 17440:	34°25′S/18°50′E	400 m	1 ♀	7,7 mm

Holotype

Unique adult female, deposited in the South African Museum, number SAM A13436.

Description

Adult female, length 7,7 mm. Body smooth, integument very finely squamous. Dorsal outline of carapace gently arched, not carinate or serrate (Fig. 15A). Pseudorostrum very short, meeting just in front of minute, triangular eyeless eyelobe (Fig. 15C). Antennal notch relatively deep, antero-lateral angle with a small tooth (Fig. 15B). Carapace $\frac{2}{3}$ as deep as long, and just longer than remaining free thoracic somites. Terga of second, third and fourth pedigerous somites slightly elevated, the second most obviously. Cephalothorax just shorter than abdomen. Telsonic somite only slightly produced between uropods.

Antenna 1 (Fig. 15D) short, basal segment robust, $\frac{3}{4}$ as broad as long with a row of six small denticles along outer edge. Second segment $\frac{1}{3}$ length of first, and broader than long. Third segment nearly twice length of second. Flagellum

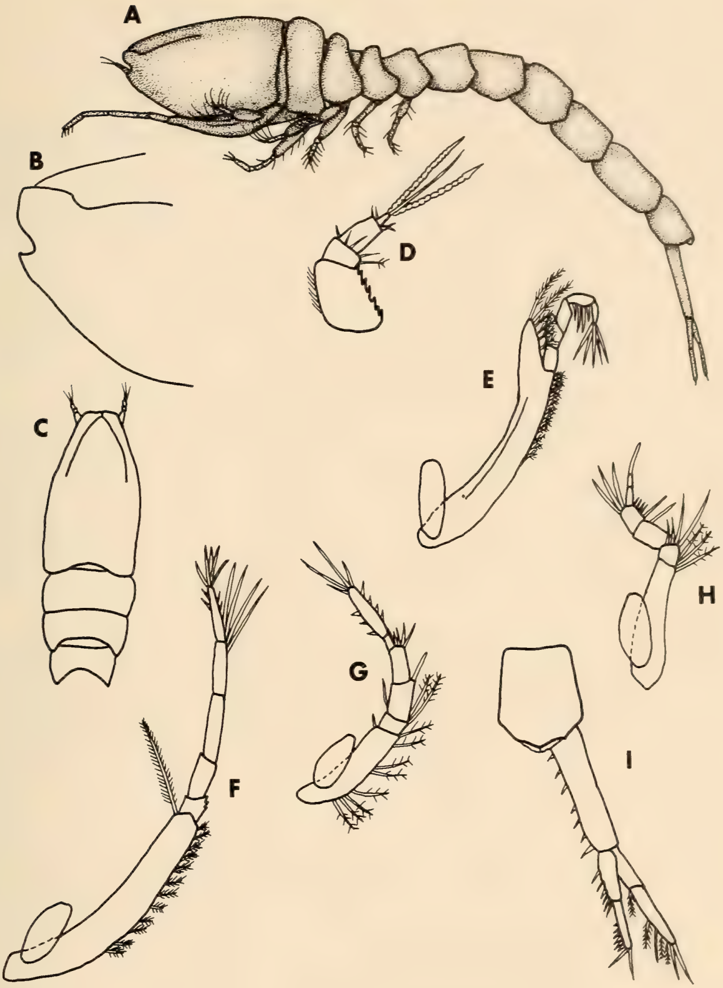

Fig. 15. *Bathycuma datum* sp. nov.
Adult female, holotype, 7,7 mm: A, lateral view; B, detail of anterior end of carapace; C, dorsal view of carapace; D, antenna 1; E, maxilliped 3; F, pereiopod 1; G, pereiopod 2; H, pereiopod 3; I, telsonic somite and uropod.

1-segmented with two terminal aesthetascs. Accessory flagellum 1-segmented, and half as long as flagellum.

Mandible normal, with narrow base.

Basis of maxilliped 3 (Fig. 15E) (including distal prolongation) twice length of remaining segments. Prolongation of basis narrow, extending not quite to distal end of merus. Ischium nearly twice as long as broad, merus slightly longer than ischium, slightly expanded internally. Basal segment of exopod less than $\frac{1}{3}$ length of basis.

Pereiopod 1 (Fig. 15F) elongated, basis just shorter than remaining segments. Ischium square with two small denticles distally. Merus twice length of ischium. Carpus equal to ischium plus merus. Propodus and dactyl subequal. Basal segment of exopod less than $\frac{1}{3}$ length of basis.

Basis of pereiopod 2 (Fig. 15G) just longer than next four segments. Ischium $1\frac{1}{2}$ times as broad as long, merus twice this length. Merus and carpus subequal, propodus small. Dactyl almost as long as merus plus carpus, setiferous, with four very stout terminal spines. Basal segment of exopod more than half length of basis.

Pereiopod 3 (Fig. 15H) with basis longer than remaining segments. Ischium square, merus twice its length. Propodus and dactyl almost subequal, each $\frac{2}{3}$ length of carpus. Basal segment of exopod less than half length of basis.

Pereiopods 4 and 5 similar, but basis of pereiopod 4 longer.

Peduncle of uropods (Fig. 15I) $1\frac{1}{2}$ times length of telsonic somite and just longer than exopod, with seven evenly spaced spines along inner edge. Endopod just shorter than exopod, segments subequal, first with six fine spines on inner edge, second with six small spines on inner edge and two long terminal spines. First segment of exopod $\frac{2}{3}$ length of second, unarmed. Second with four plumose setae and one spine on inner edge, and two spines terminally.

Remarks

This species may be distinguished from others of the genus by the absence of a serrated dorsal carina, the short, stout first antenna with a 1-segmented flagellum, and the relatively short prolongation of the telsonic somite between the uropods.

Distribution of Bathycuma

As the name *Bathycuma* indicates, most of the species in this genus inhabit waters of a considerable depth—usually more than 1 000 m. The genus is quite widely distributed in the North Atlantic, Mediterranean, Indian and Pacific Oceans, generally being circumtropical, with certain elements from higher latitudes. The three South African species would appear to have been derived from the Indian Ocean group, rather than having spread from the North Atlantic, since no species have been found on the west coast of Africa. All three are endemic, *B. capense* to the west coast, *B. natalense* to the south and east coasts, and *B. datum* to the Cape west of the Peninsula. The known depths at which all three species occur are unusually shallow for the genus.

DISTRIBUTION OF THE VAUNTHOMPSONIINAE

In general the distribution of each species in the subfamily is rather narrow. This is partly due to rather scanty collecting in many areas, but even taking this into account, of the 65 species listed in Jones (1969) and the present work, only one, *Vaunthompsonia cristata*, is found in the Atlantic, Indian and Pacific Oceans, one in the Pacific and Indian Oceans (*Heterocuma sarsi*), one in the

Atlantic and Pacific Oceans (*Cumopsis goodsiri*), and one in the Indian and Atlantic Oceans (*Heterocuma africanum*)—a total of less than 7% of the species in the subfamily occurring in more than one ocean.

Zimmer (1941) has called the Bodotriidae a 'negatively amphipolar' family. This is borne out by the fact that none of the Vaunthompsoniinae has been found at latitudes greater than 70°. Table 1 details the distribution of the subfamily. Each species may be represented more than once, as each record of a species from widely differing areas has been included.

TABLE 1

Distribution of Vaunthompsoniinae according to depth and latitude. Data mainly from Jones (1969).

Latitude	*Shore–5 m*	5–200 *m*	200–2 000 *m*	>2 000 *m*	*Total number*
N of 70°N	—	—	—	—	—
70°N–50°N	1	4	—	—	5
50°N–20°N	3	13	5	1	22
20°N–20°S	1	13	3	1	18
20°S–50°S	2	36	4	2	44
50°S–70°S	—	2	—	1	3
S of 70°S	—	—	—	—	—
Total	7 (5 sp)	68 (47 sp)	12 (10 sp)	5 (5 sp)	92 (67 sp)

Only eight of the 92 records are from latitudes greater than 50°. The majority of records are from 20° to 50° N and S, fewer being found in the tropics, which is generally true for the Cumacea. The predominance of records in the south temperate latitudes may be due to the very extensive work done by Hale in Australia. 21 of the 44 records for these latitudes are his, and as few other areas have been as thoroughly worked, the data are somewhat biased in this direction. However the bias is offset to some extent by the fact that only one member of the subfamily has been described from the whole of South America, where very little collecting has been done. Assuming that more records will eventually come from this region, it may be concluded that the Vaunthompsoniinae are a family of temperate latitudes, predominating in the south.

Again, 81% of the records are from depths less than 200 m, indicating that the subfamily belongs predominantly to the shelf fauna, with some elements, particularly members of the genus *Cumopsis*, now occupying the infratidal fringe, and some, particularly *Bathycuma* and *Gaussicuma*, the bathyal and abyssal zones.

DISTRIBUTION OF THE SOUTH AFRICAN VAUNTHOMPSONIINAE

The southern African coast is washed on the western side by the cold northward-flowing Benguela Current (surface 15°C, bottom 10°C), and the warm Moçambique Current flowing southwards along the east coast (surface 25–27°C, bottom 21°C). The southern coast has the fast-flowing warm Agulhas Current running from north-east to south-west (surface 25°C, bottom 12–14°C), and a narrow counter-current close inshore. The Cape Peninsula marks the westward extent of the warm tongues of Agulhas water which occasionally penetrate into False Bay (surface 15°C, bottom about 12°C). The boundary between Agulhas and Benguela water is not stationary, so that False Bay may also receive cold Benguela water at other times of the year. Thus generally animals from the west coast are cold-water forms, and those from the south and east coasts (including False Bay), warm-water forms. It is frequently found that animals occurring in fairly shallow water on the cold west coast inhabit deeper waters on the south coast due to the increased temperature of the Agulhas water (Day *et al.* 1970). Seven of the eleven species and subspecies of Vaunthompsoniinae in these waters are confined to one or other coast, suggesting that their distribution may be largely temperature-dependent.

The only inter- and infra-tidal species, *Cumopsis robusta*, which belongs to a predominantly intertidal genus, has only been found in False Bay and on the west coast, and is therefore endemic. The anatomically related *Heterocuma* is a shelf genus. *H. africanum intermedium* occurs in fairly large numbers in False Bay (maximum depth just less than 90 m) to a depth of 66 m, and has also been found in 27 m on the west coast. The same species has also been recorded twice from the south coast in 84 to 91 m—an example of shallower depth range on the west coast. It has also been recorded from shallow waters off tropical West Africa. It is thus a warm-water Atlantic form, and is the only species represented by more than 12 specimens in the present collection. *H. africanum africanum* has only been found off Natal in 43 m, as well as in the Indian Ocean and tropical West African waters.

Pseudosympodomma africanum is endemic, being found at a depth of 370 m off the Cape Peninsula, and also at 85 and 135 m off the east coast.

The *Bathycuma/Hypocuma/Vaunthompsonia* group is divided not only taxonomically but also ecologically, *Bathycuma* generally occurring at very great depths, the two species of *Hypocuma* at 400 and 1 934 m and *Vaunthompsonia* at less than 250 m. *Bathycuma*, represented by three species and 17 specimens, can be divided into a group living in fairly deep water off the Cape (*B. datum* and *B. capense*), and *B. natalense* with the rather peculiar depth distribution from 15 to 400 m off Natal. The depth range of all three species is rather shallow, since *Bathycuma* is generally a typically bathyal genus. *Hypocuma dentatum*, represented by only four specimens in a single sample, appears to be a deep-water endemic form. Although three species of *Vaunthompsonia* are present, they are represented by only six specimens, so that numerically, members of the genus are only scantily represented in these waters. The three species do not overlap in range, and the distribution of each necessarily appears narrow due to the paucity of specimens. *V. natalensis* has been found only on the south and east coasts, *V. cristata* in False Bay, and *V.* sp. on the west coast.

Thus the fauna can be divided into three groups:

1. Cold-water forms occurring on the west coast only—*Hypocuma dentatum*, *Bathycuma datum* and *Vaunthompsonia* sp.

2. Warm-water forms occurring on the south and east coasts only—*Bathycuma natalense*, *Vaunthompsonia natalensis* and *Heterocuma africanum africanum*.
3. Forms occurring around the coast, or including False Bay in their range—*Pseudosympodomma africanum*, *Bathycuma capense*, *Vaunthompsonia cristata*, *Heterocuma africanum intermedium* and *Cumopsis robusta*.

The present collection contains at least two thousand specimens of the Bodotriidae. All but 77 of these are Bodotriinae, representing an estimated 18–20 species, giving a specimen : species ratio of at least 100 : 1. The 77 Vaunthompsoniinae represent 11 species, giving a very high ratio of 7 : 1. Thus the subfamily exhibits a very high diversity in these waters. There is also a high rate of endemism. Of the ten named species and subspecies, only three—*Vaunthompsonia cristata*, *Heterocuma africanum africanum* and *H. a. intermedium*—are not endemic. Thus 70% of the species are endemic, with a link to the tropical West African fauna in the form of the two subspecies of *H. africanum*, while *V. cristata* is cosmopolitan.

SUMMARY

Nine species of the southern African members of the subfamily Vaunthompsoniinae are described and figured. Of these, *Hypocuma dentatum*, *Cumopsis robusta*, *Bathycuma datum* and *Vaunthompsonia natalensis* are new species. *Heterocuma africanum africanum* and *H. a. intermedium* are newly designated subspecies. The females of *Bathycuma capense*, *B. natalense* and *Pseudosympodomma africanum* are described for the first time, *P. africanum* also being allocated to a different genus. A specimen of *Vaunthompsonia* is briefly described and figured, but not named. It is found that the subfamily is represented in southern Africa by ten species in six genera.

The general distribution of the Vaunthompsoniinae is discussed, and a more detailed account is given of the distribution of its southern African members. It is concluded that this subfamily in southern African waters has a high rate of endemism and a high diversity, but a very low frequency of occurrence.

ACKNOWLEDGEMENTS

I should like to thank Dr R. R. Given of the Allan Hancock Marine Foundation, California, for his help, advice and encouragement; Dr M. Băcescu of the Musée d'Histoire Naturelle, Bucharest, for providing specimens of *Cumopsis fagei* and literature, and Dr N. S. Jones of the Marine Biological Station, Isle of Man, for specimens of *C. fagei*. I am also very grateful to Dr Brian Kensley of the South African Museum, Cape Town, for material and for tracing *Pieter Faure* station data, and Mr Tim McClurg of the National Institute for Water Research, Durban, for material. My special thanks go to Professor J. H. Day of the Department of Zoology of the University of Cape Town, for discussions of taxonomic problems, and for his constructive criticism of the manuscript.

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INSTRUCTIONS TO AUTHORS

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Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

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Thiele, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* Schultze, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika.* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

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A NEW SPECIES AND RECORDS OF *SCUTELLIDIUM* (COPEPODA HARPACTICOIDEA) FROM SOUTH AFRICA, AND A WORLD KEY TO THE GENUS

By

G. M. BRANCH

Cape Town Kaapstad

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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(1–2, 5, 7–9),
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11(1–2, 5, 7, t.–p.i.), 24(2), 27, 31(1–3), 33

Price of this part/Prys van hierdie deel
R1,75

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ISBN 0 949940 62 3

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

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By

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Zoology Department, University of Cape Town

(With 24 figures)

[*MS accepted 1 July 1974*]

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INTRODUCTION

The genus *Scutellidium* Claus, 1866 now comprises 25 species, of which *S. sarsi* and *S. digitatum* are of uncertain position (and are not included in the key given here). These are all listed or described by Lang (1948, 1965), Vervoort (1964), Hicks (1971) and Branch (1973).

The present collection, made at Kalk Bay in the Cape Peninsula of South Africa (34°8′S/18°27′E), includes three species: *S. patellarum* (Branch 1973), *S. ringueleti* and a new species, described below as *S. macrosetum* sp. nov.

METHODS

All material was obtained from alcohol washings of intertidal algae, preserved in 70% alcohol and then dissected and mounted in a glycerine-formalin mixture. Drawings are based on camera lucida projections. The following abbreviations have been used: A1 and A2, Antenna 1 and 2. End., endopodite; Exp., expodite; P1–5 swimmings legs 1–5; Segmt., segment. Student's t test has been used to compare mean lengths, and where relevent, 95% confidence limits have been given for mean values.

Scutellidium macrosetum sp. nov.

Female

Live material pale yellow-brown. Length (rostrum to furcae): 0,738 mm, range: 0,690 to 0,780 mm based on 15 specimens. Body compressed dorsoventrally. Prosoma oval but truncated posteriorly (Fig. 1). Posterior corners

Ann. S. Afr. Mus. **66** (10), 1975: 221–232, 24 figs.

of prosomal segments forming rounded epimera: those of the 3rd segment expanded and about twice the size of the other segments (Fig. 2). Prosoma naked. Urosome 5 segmented, the genital 'double segment' very swollen and almost twice the width of the other segments (Fig. 3). Tufts of setae on the posterior—lateral margins of all but the last segment. Furcal rami about as long as wide, with two very long and four shorter setae. Rostrum (Fig. 4) rounded and naked except for two pairs of slender filaments (which are frequently invisible).

A1 9 segmented and stout: similar to that of *S. armatus* (Wiborg, 1964), except that segment 4 is shorter and wider. Segment 1 stout and well developed; segment 2 about 2½ × length of segment 3; segments 4–7 short and broad, telescoped together, making the setal arrangement difficult to determine accurately (Fig. 5). The basal segment has a characteristic strongly plumose seta (Fig. 5a), one of the readily identifiable features of the species. Some of the setae on segment 2 are also setose. The relative lengths and armature of the segments appear in Table 1.

TABLE 1. Details of A_1

	Segment	1	2	3	4	5	6	7	8	9	Total
♀	Length μ	93	98	42	13	7,5	5,7	7,5	19	42	327
	Relative length	29	30	13	4	2	1,5	2	5,5	13	100
	Setae	1	13	?5	?5+A	3	1	2	2	4	36
♂	Length μ	60	80	23	34	23	38	11	26		295
	Relative length	20	27	7,5	11,5	7,5	13	4	9		100
	Setae	1	11	9	5+A	2	1	2	5		36

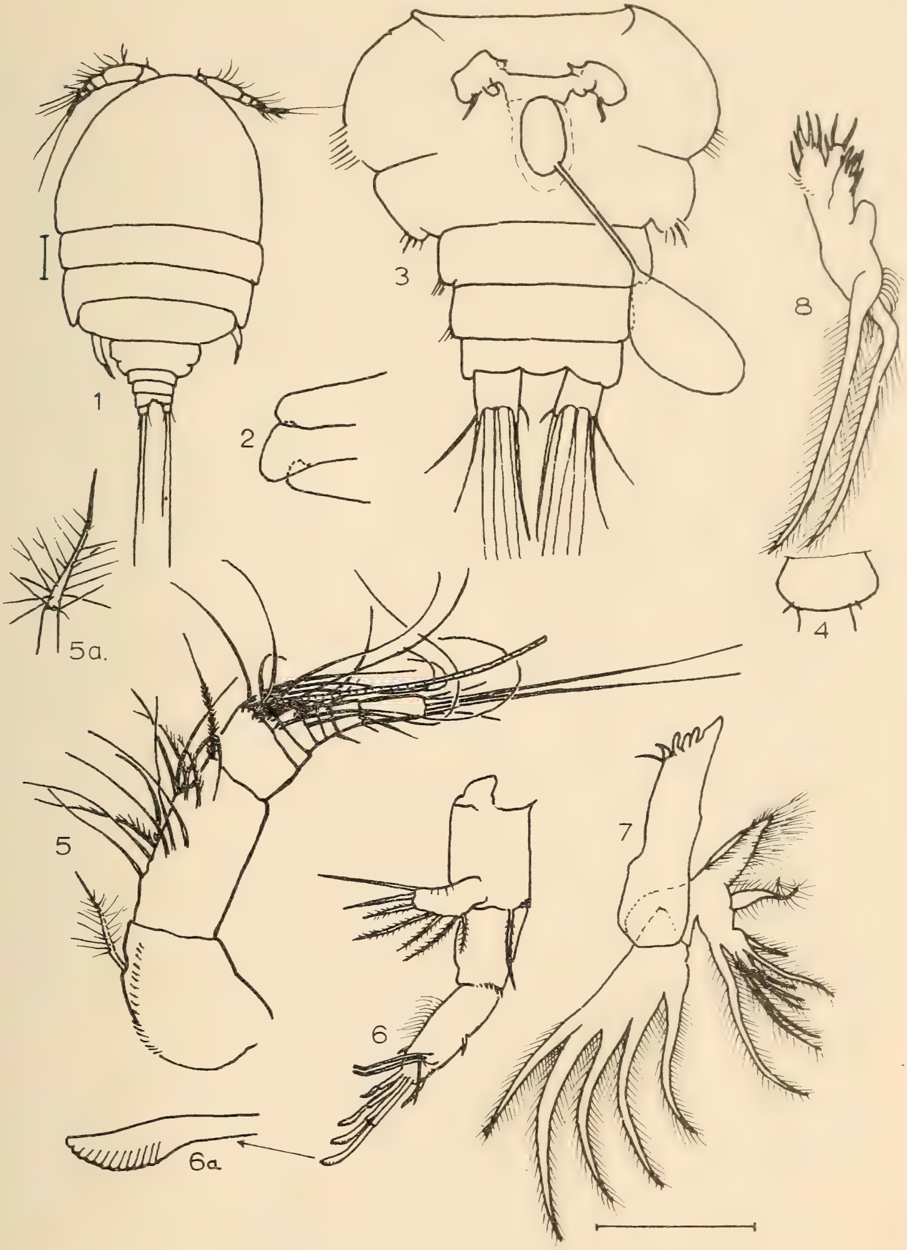
A2 basipodite with a single seta (Fig. 6). End 1 naked except for terminal spinules, end 2 with setae and spines (see Fig. 6). Exp. weakly segmented, with 7 setae, the terminal 2 naked and the others shortly plumose.

Mandible (Fig. 7) and maxilla (Fig. 8) almost identical to *S. armatus*. Maxilla 2 (Fig. 9) with a single segmented syncoxa bearing a shortly plumose seta. No basal endite or setae on the syncoxa (but as these are difficult to dissect out intact they may have been lost); a small distal endite with two setae.

Maxilliped (Fig. 10) 3 jointed, the basal segment with a long seta, the 2nd joint not as expanded as in most other species, and the terminal joint with a stout toothed claw and 3 setae.

P1 (Fig. 11) exp. and end. very broadly expanded, exp. about same length as end. segment 1. Exp. 1 nearly as broad as end. 1; exp. 2 about half the size, with 2 long internal setae and one short external seta. Exp. 3 characteristically extremely small, with 4 small penicillate setae and one very long seta. End. 1 with a large inner seta arising just below the midpoint, and a semi-elliptical row of setules. End. 2 about half the length and with a single short inner seta. End. 3 small, carrying 2 penicillate setae which conceal a small straight plumose seta. Basis with a broad outer seta and a small curved inner seta.

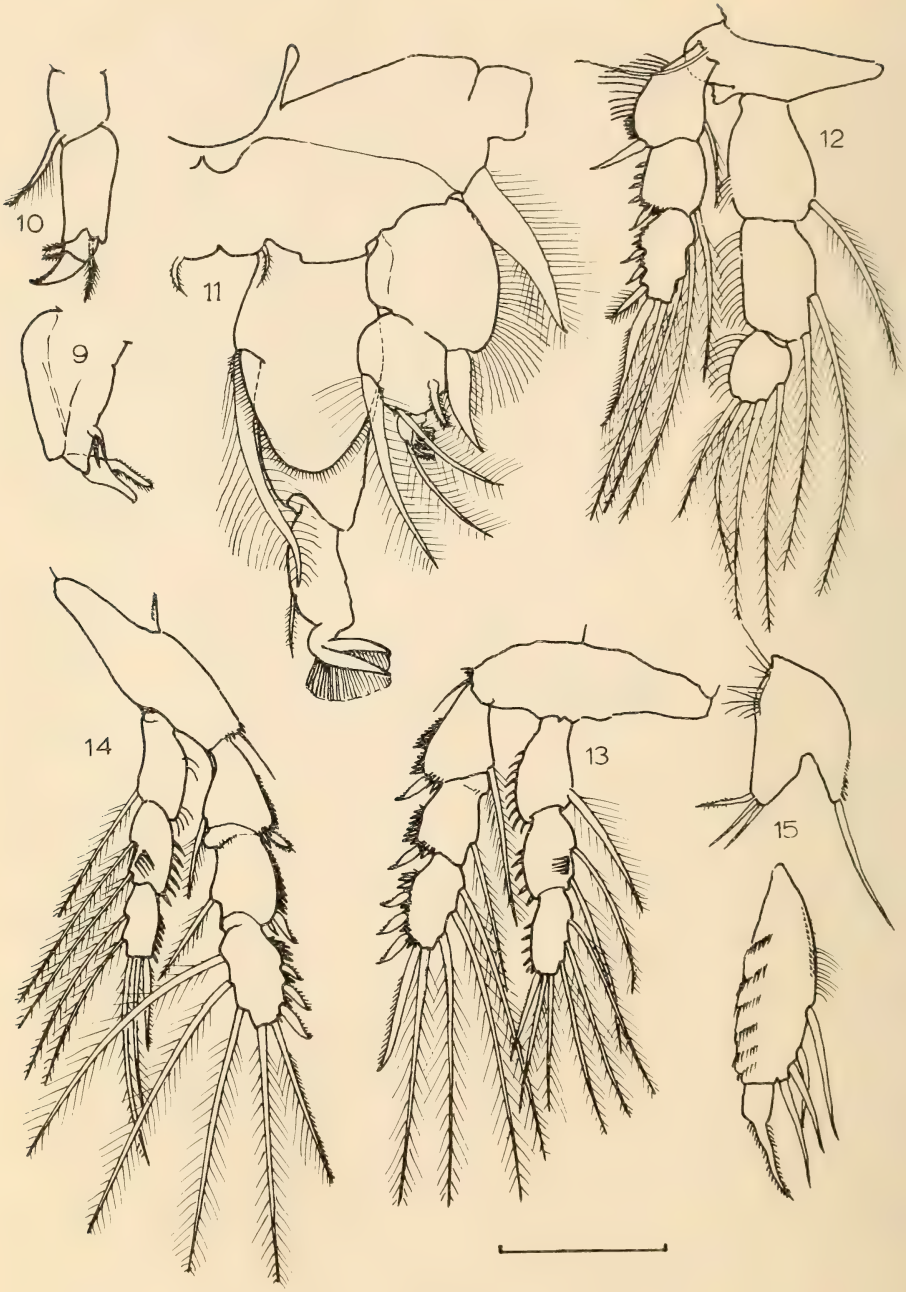
P2 (Fig. 12): end. 2 almost as long as wide. A slender outer seta on the basis. End. 3 with only 4 setae.



Figs 1–8. *Scutellidium macrosetum* sp. nov. ♀

1. Dorsal view of ♀.
2. Epimera of segments 2, 3 and 4.
3. Ventral view of urosome.
4. Rostrum.
5. Antenna 1.
6. Antenna 2.
7. Mandible.
8. Maxilla 1.

Both scales indicate 100 μ.



Figs 9–15. *S. macrosetum* ♀

9. Maxilla 2. 10. Maxilliped.
11–14. Swimming legs 1 to 4. 15. P5.
The scale indicates 100 μ.

P3 and P4 as in Figures 13 and 14.

P5 (Fig. 15) with a bilobed basoendopodite, inner lobe with 3 setae, outer with one longer seta. Exp. with a characteristic terminal setae, which is very swollen at the base and distally tapered and bipectinate. (The specific name *macrosetum* is derived from this). In addition there are 4 marginal setae of approximately the same length (in one animal the 3rd marginal was half the length of the other setae), and six parallel rows of setules.

Male

Similar to ♀ but smaller, length 0,645 mm, (range 0,615–0,675, based on 3 specimens). Urosome much more slender and clearly 5 segmented. First segment with dorso-lateral lobes (Fig. 16) which project posteriorly, partly covering P5 and P6. Segments 2–4 each overlap the subsequent segment ventrally, forming a spinule fringed flange (Figs 16, 17).

Apart from A1, P5 and P6 all appendages very similar to those of the ♀.

A1 (Fig. 18) 8 segmented, the basal segment also bearing a strongly plumose seta. Segment lengths and armature given in Table 1 and Figure 19a–c.

P5 (Fig. 20) basoendopodite not as well defined as in the female: inner lobe small, with 1 seta flanked by two small setules. Outer lobe larger, with 1 seta and a row of setules. Exp. again with a large terminal seta which is swollen at the base and bipectinate. Outer margin with 4 setae of roughly equal length, and a fringe of setules. (This is the only species in the genus in which the ♂ has 5 setae on P5 exp.)

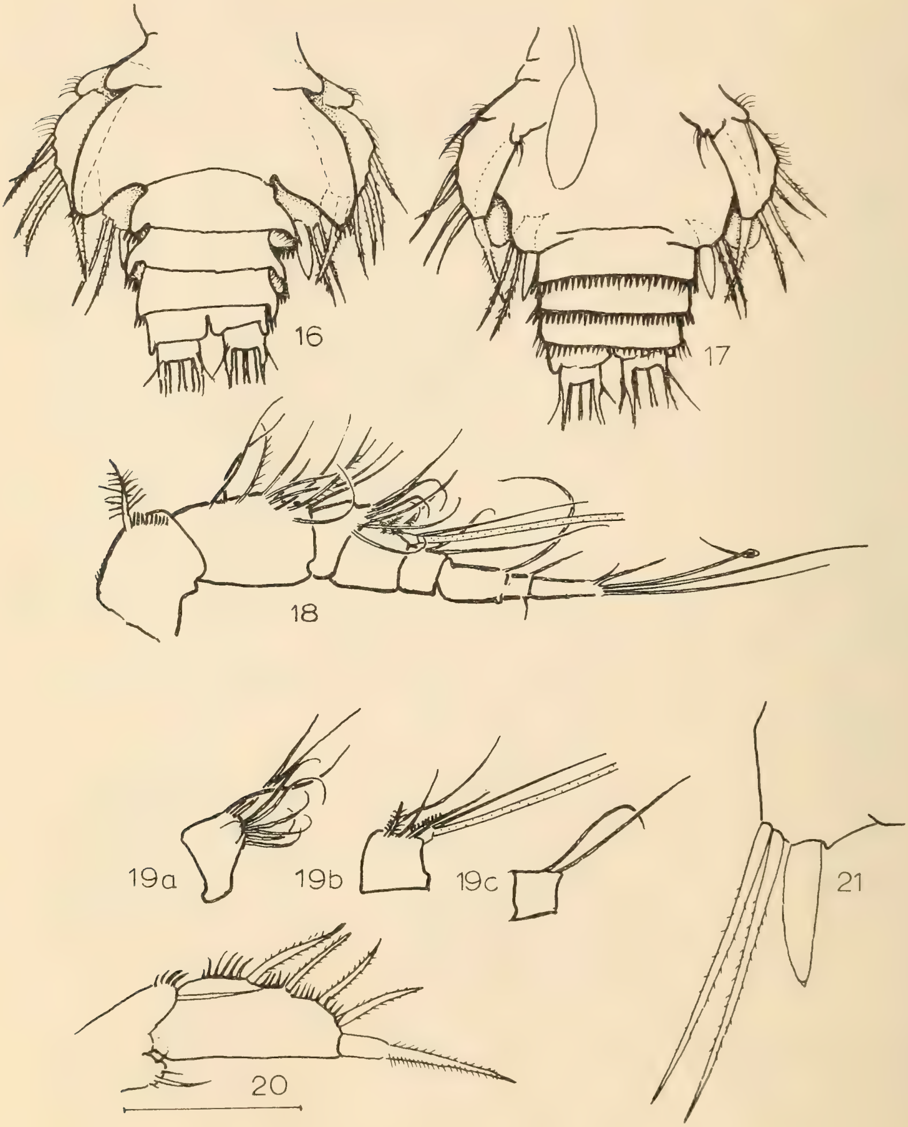
P6 a conical projection (Fig. 21) with a single stout blunt seta and two slender setae about twice the length.

Affinities

S. macrosetum is closely allied to *S. armatus* (Wiborg), the only member of the genus with which it can be confused. The easiest distinguishing factor is that *S. macrosetum* has 5 setae on P5 in both sexes while *S. armatus* has 4. (The possibility that *S. armatus* was incorrectly described and had simply lost one seta, can be discounted as both Wiborg (1964) and Pallares (1969: pl. 1, figs 2, 11), describe both sexes as having only 4 setae on P5.)

Other differences are summarized below.

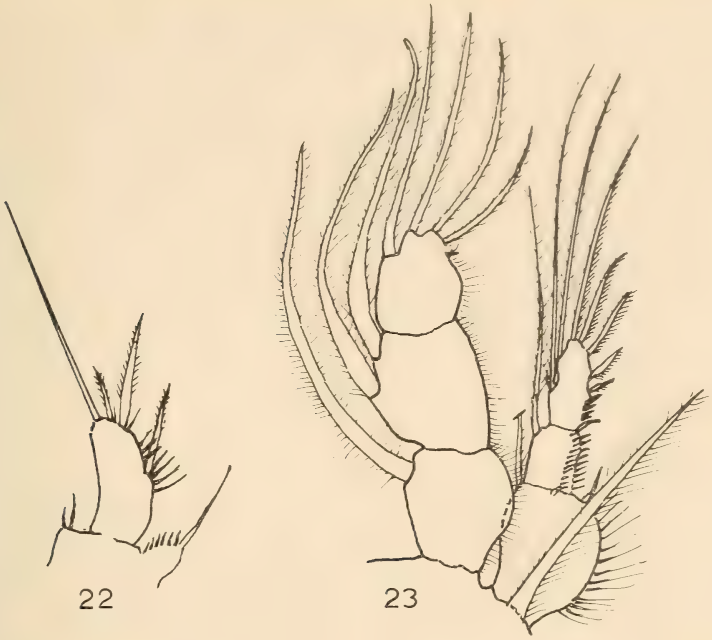
	S. macrosetum	*S. armatus*
1. Inner seta, P1 basis	Slender and curved	Broad and 'knife-shaped'
2. Relative width of P1 End. 1 : P1 exp. 1	1 : 1	2 : 1 (Pallares 1969) ?1½ : 1 (Wiborg 1964)
3. Relative length of P1 exp. 2 : P1 exp. 3	3½ : 1	2 : 1
4. Shape of P5 ♀ terminal seta	Base bulbous, terminal part tapering	Broad and curved tapering gradually
5. ♀ P5 no. of setae	5	4
6. ♂ P5 no. of setae	5	4
7. P1 exp. 2, setae	3 : broad inner, stubby outer and terminal long and slender.	2 : broad inner and stubby outer (Pallares 1969)
8. P5 ♀. 6 parallel rows of setules	present	absent



Figs 16–21. *S. macrosetum* ♂

16, 17. Dorsal and ventral views of the urosome.
18. Antenna 1. 19a, b, c. Segments 3, 4, 5 of antenna 1.
20. P5. 21. P6.

Scale indicates 100 μ, and applies to all the figures except Fig. 21 which is twice the size.



Figs 22–23

22. *Scutellidium ringueleti* ♂ P5.
23. *S. ringueleti* ♀ P2.

S. macrosetum can be distinguished by the following combination of features: P5 exp. with 5 setae, the terminal seta swollen at the base and pectinate; furcal rami as long as wide; P1 end. 1 about 2 × length of end. 2; P2 end. 2 nearly twice as long as wide; P1 exp. about same length as P1 end. 1; basal segment A1 with a very strongly setose seta.

Material

Dissected holotype (♀) and allotype (♂) and intact paratypes (15 ♀♀ and 3♂♂) have been deposited in the South African Museum, Cape Town. (Catalogue numbers S.A.M. A13599, A13600, A13601).

Scutellidium ringueleti Pallares, 1969

Material

55 ♀♀ (length 0,55–0,95 mm) and 14 ♂♂ (length 0,55–0,80 mm) collected at low tide level on *Gigartina stiriata* and *Bifurcaria brassicaeformis*.

Known distribution

Ria Deseado, Patagonia.

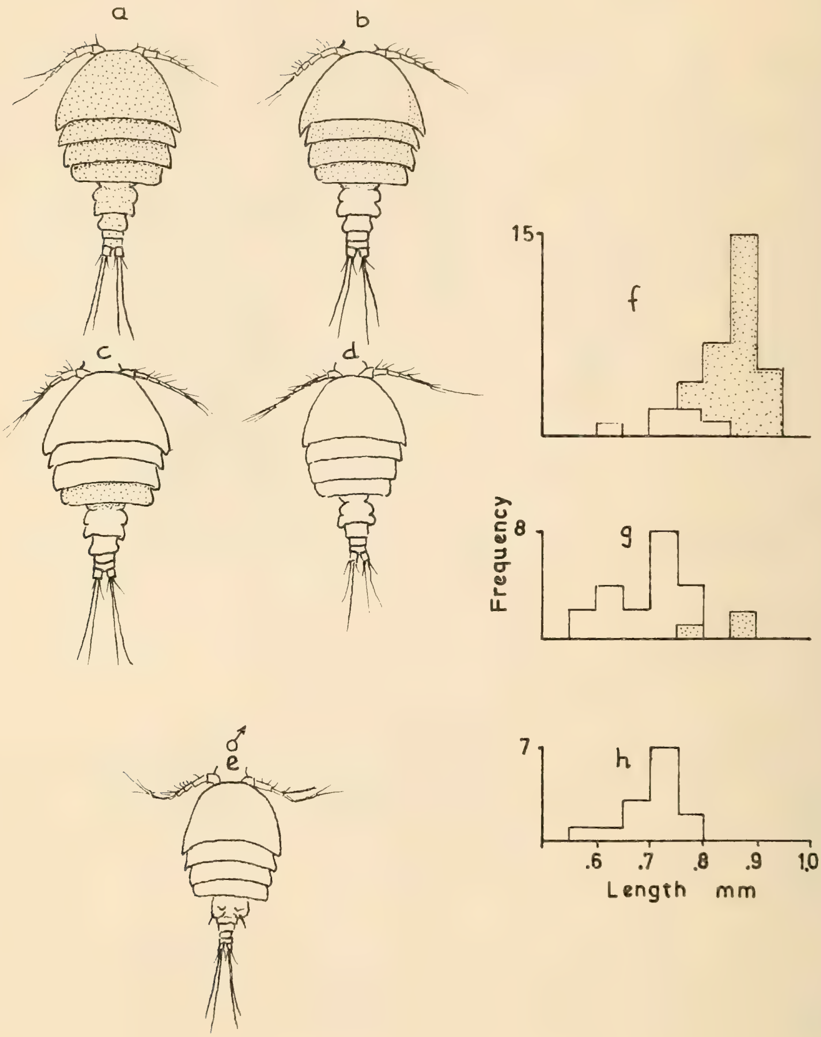


Fig 24. Size and colour variations in *S. ringueleti*, in relation to foodplant. Shading indicates a purple coloration.

a–d: ♀ colour variations. e: ♂. f: size distribution of ♀♀ collected on *Gigartina*. g: size distribution of ♀♀ on *Bifurcaria*. h: size frequency of ♂♂.

Discussion

The present material agrees almost exactly with the excellent description given by Pallares (1969), except for a few minor particulars: the terminal seta of ♂ P5 much longer—about 2,5 × length of the exp. (Fig. 22); ♀ P5 terminal seta, two thirds length of adjacent seta; maxilliped end. 1 with a proximal marginal spine (often not visible); outer seta on basis of P2 extending just beyond tip of exp. (Fig. 23), but rather variable in length.

Many of these features are intermediate between those of *S. ringueleti* and the closely allied *S. spinatum* from New Zealand. Both these species have been described in detail and the differences between them are slight (see Hicks 1971: 92). The intermediate nature of the South African material makes it even more difficult to separate the species, and it seems probable that *S. spinatum* is synonymous with *S. ringueleti.* A direct comparison of the material is required.

Colour varieties

The South African material contains several colour varieties of *S. ringueleti:* Light yellow brown (58%); brown with a deep purple strand across the last free metasomal segment and the first urosomal segment (32%); brown with the last 3 metasomal segments and the epimera deep purple (3%); entirely purple (7%).

These are of interest because Monk (1941) has used similar colour variations to recognize varieties and species. *Scutellidium arthuri* var. *magna* Monk, 1941 is distinguished from the typical form by its greater size (1,4 mm as compared with 0,91 mm) and the presence of a deep purple band on the 'first free segment of the metasome and on the urosome.' Lang (1965) considers the variety invalid. Monk has also described a closely allied species *S. purpurocincta*, distinguished from *S. arthuri* by its colour, 'purple on the 3 free segments of the metasome' (Monk 1941: 96), and the proportionally longer third segment of A1. Lang (1965: 151) also doubts the validity of this species.

As in Monk's case, the present purple varieties of *S. ringueleti* are significantly larger than the 'typical' brown form: 0,85 ± 0,02 compared with 0,69 ± 0,04 (significantly different at $p < 0{,}001$).

Further samples of *S. ringueleti* show that the purple and brown varieties were associated with different foodplants, respectively *Gigartina stiriata* (Rhodophyta) and *Bifurcaria brassicaeformis* (Phaeophyta). Figure 24 illustrates the relationship between copepod size and colour, associated with these two algae. Clearly such colour and size variations are phenotypic and related to the foodplant: they are valueless in distinguishing taxonomic varieties. Curiously, the males displayed no such variations and were all small and light brown. This parallels Monk's case again, for he found no males corresponding to the purple forms, *S. arthuri magna* or *S. purpurocincta.*

In the light of this the variety *magna* cannot be justified, and further doubt is cast on the validity of *S. purpurocincta.*

KEY TO THE WORLD SPECIES OF *SCUTELLIDIUM*

♀♀

1. Furcal rami as long as wide or wider than long 4
Furcal rami longer than wide 2
2. Exp. P5 long: 4 × longer than wide . . . . . *S. lenticulare* (Brady, 1910)
Exp. P5 shorter: less than 3 × longer than wide 3
3. Exp. P5 with transverse rows of spinules; A1 segment 2 1,25 × length of segment 3 *S. antarcticum* (Lang, 1936)
Exp. P5 without transverse rows of spinules; A1 segment 2 and 3 subequal *S. major* (T. Scott, 1912)
4. External seta on P2 basis strongly increased in size: more than $\frac{2}{3}$ length of exopod . 5
External seta on P2 basis, normal: less than $\frac{1}{2}$ length of exp. 13
5. P1 end. 1 roughly same length as end. 2 6
P1 end. 1 at least $1\frac{1}{2}$ × length of end. 2 7
6. P2 seta on basis does not reach tip of exp.; maxilliped end. 1 with 2 marginal spines and 3 rows of spinules . . . . . *S. spinatum*[1] Hicks, 1971
P2 seta on basis extends beyond tip of exp.; maxilliped end. 1 with no marginal spines and 1 row of spinules . . . . . *S. ringueleti*[1] Pallares, 1969
7. Outer spines of P2 end. setiform, and $1\frac{1}{2}$ to 2 × length of segments bearing them *S. patellarum* Branch, 1973
Outer spines of P2 end. short, normal 8
8. P1 end. 1, about $1\frac{1}{2}$ × length of end. 2 9
P1 end. 1, 2 or more × length of end. 2 10
9. P1 exp. 2 strongly swollen internally, seta arising from centre of swelling *S. plumosum*[2] Brady, 1899
P1 exp. less strongly swollen, and seta arising distal to swelling *S. intermedium*[3] (Nicholls, 1941)
10. P1 end. 1, 3 × length of end. 2 . . . . . *S. strigosum* Pallares, 1969
P1 end. 1, 2 × length of end. 2 11
11. P2 end. 2 as long as wide . . . . . *S. arthuri*[4] Poppe, 1884
P2 end. 2 longer than wide 12
12. A1 segments 2 and 3 similar in length (proportions 13 : 11) *S. purpurocincta*[4] Monk, 1941
A1 segment 2 obviously longer than 3 (proportions about 17 : 11) *S. dentipes*[4] Vervoort, 1964
13. P1 exp. 1 same length as P1 end. 1 . . . . . *S. ligusticum* (Brian, 1920)
P1 exp. 1 shorter than end. 1 14
14. P5 terminal seta much wider than other setae, and setose 15
P5 terminal seta not as above 16
15. P5 exp. with 4 setae . . . . . *S. armatus* (Wiborg, 1964)
P5 exp. with 5 setae . . . . . *S. macrosetum* sp. nov.
16. P3–4 end. 2 with 1 seta . . . . . *S. hippolytes* (Krøyer, 1863)
P3–4 end. 2 with 2 setae 17
17. P5 exp. with at least 3 terminal setae 18
P5 exp. with 1 terminal seta (others marginal) 20
18. P5 basoendopodite inner lobe with 3 setae . . . . . *S. idyoides* (Brady, 1883)
P5 basoendopodite inner lobe with 2 setae 19
19. P5 exp. inserting with a broad base, internal and external walls nearly parallel, so the exp. is elongate; P1 end. 2, inner seta arises nearer distal end of segment *S. cockburni* Fairbridge, 1944
P5 exp. narrow at base and apex, margins convex and exp. oval; P1 end. 2 inner seta arises nearer proximal end of segment . . . . . *S. australe* (T. Scott, 1912)
20. P5 exp. with 2 short thick setae: 1 terminal and 1 external, and with marginal spinules and transverse rows of spinules . . . . . *S. fuciculum* (T. Scott, 1912)
P5 exp. with 5 distinct setae 21
21. P5 terminal seta short, $< \frac{1}{3}$ length of exp.; coxa of maxilliped without a spine *S. longicauda* (Philippi, 1840)
P5 terminal seta longer at least $> \frac{1}{2}$ length exp.; exp. length $< 3 \times$ width . . . 22
22. P5 terminal seta about $\frac{2}{3}$ length of adjacent seta, and swollen at base; coxa of maxilliped with an internal spine . . . . . *S. deseadensis*[5] Pallares, 1966

♀♀

P5 terminal seta elongate, same length as adjacent seta, not swollen at base; coxa of maxilliped with internal spine . . . . *S. loureiroi*[5] Jakobi, 1954

P5 terminal seta elongate, slightly longer than adjacent seta, not swollen at base. (Maxilliped undescribed.) No external seta at base of P2 end. (?) *S. lamellipes*[5] Monk, 1941

♂♂

1. Exp. P5 with 3 spines or setae 2
   Exp. P5 with 4 spines or setae 3
   Exp. P5 with 5 spines or setae . . . . *S. macrosetum* sp. nov.
2. P1 end. 1 almost 2 × length end. 2 . . . . *S. longicauda* (Philippi, 1846)
   P1 end. 1 not much longer than end. 2 . . . . . . *S. intermedium* (Nicholls, 1941)
3. Outer spines P2 exp. setiform and about 1½ to 2 × length of the segments bearing them *S. patellarum* Branch, 1973
   Outer spines P2 exp. short 4
4. P1 end. 1 roughly same length as end. 2 5
   P1 end. 1 at least 1½ × length of end. 2 9
5. One of the setae on P5 exp. lancet-shaped 6
   All setae on P5 exp. normal 7
6. P1 end. 1 almost same length as exp. 1 . . . . *S. ligusticum* (Brian, 1920)
   P1 end. 1 about 1½ × length of exp. 1 . . . . *S. australe* (T. Scott, 1912)
7. P3–4 end. 2 with 1 seta . . . . *S. hippolytes* (Krøyer, 1862)
   P3–4 end. 2 with 2 setae 8
8. P5 exp. with rows of small spinules at base;
   P2 seta on basis not reaching beyond tip of exp. . . . . . *S. spinatum*[1] Hicks 1971
   P5 exp. without rows of spinules at base;
   P2 seta on basis reaches beyond tip of exp. . . . . . . *S. ringueleti*[1] Pallares 1969
9. External seta on basis of P2 elongated, at least ½ length of exp. 10
   External seta on basis of P2 short 11
10. P1 end. 1 about 1½ × length of end. 2 . . . . *S. plumosum* Brady, 1899
    P1 end. 1 about 2 × length of end. 2 . . . . *S. arthuri* Poppe, 1884
    P1 end. 1 about 3 × length of end. 2 . . . . *S. strigosum* Pallares, 1969
11. P1 exp. 1, 2 × length of exp. 2 . . . . *S. armatus* (Wiborg, 1964)
    P1 exp. 1 about same length as exp. 2 . . . . . . *S. deseadensis*[6] Pallares, 1969
    S. lamellipes[6] Monk, 1941

ANNOTATIONS

1. As described above (p. 229) these two spp. may be synonymous.

2. In Vervoort's (1964) key, *S. plumosum* is described with a normal external seta on P2 basis, but Pallares (1969: pl. 5, fig. 1) shows it as strongly developed. I have followed Pallares.

3. P2 of *S. intermedium* has not been described but as this species is very closely allied to *S. plumosum* (Nicholls, 1941) I assume that the external seta on P2 basis is similarly elongated (see note 2).

4. *S. purpurocincta* is possibly synonymous with *S. arthuri* (see discussion p. 229). *S. dentipes* may also be synonymous with *S. arthuri*, as Vervoort himself admits.

5. *S. deseadensis*, *S. loureiroi*, *S. lamellipes* are possibly synonymous. Jakobi's description is not adequate to make comparisons, and Monk's description incomplete. *S. lamellipes* can only be separated from *S. deseadensis* by 'having no spine on the second basis' of P2 (Monk 1941: 97) but as Lang (1965) points out, this statement is probably incorrect: in several species

(including *S. deseadensis*) this spine lies in a higher plane than the exp. and can be overlooked while focusing on the exp.

6. *S. deseadensis* and *S. lamellipes* are probably synonymous (see also note 5). Vervoort (1964: 106, couplet 6) describes *S. lamellipes* as having P1 end. 1 and 2 of about the same length (which would separate the two species) but this statement is doubtful, as Monk does not describe or figure this appendage, and describes *S. lamellipes* as being 'very similar to *S. longicauda*'.

SUMMARY

A description is given of *Scutellidium macrosetum* sp. nov., which is allied to *S. armatus* but distinguishable by having five setae on P5 exp. A new record and colour variations are described for *S. ringueleti*. A key is given to the known species of *Scutellidium*.

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Note added in press

Mielke (1974) has described a ♂ *Scutellidium hippolytes* with 5 setae on P5 exp. (in contradiction to Lang's (1948) description). However, this species is easily distinguishable from *S. macrosetum* by having only 1 seta on P3–4 end. 2.

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G. M. Branch

A NEW SPECIES AND RECORDS OF *SCUTELLIDIUM* (COPEPODA HARPACTICOIDEA) FROM SOUTH AFRICA, AND A WORLD KEY TO THE GENUS

VOLUME 66 PART 11 MARCH 1975 ISSN 0303-2515

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Price of this part/Prys van hierdie deel
R2,30

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ISBN 0 949940 63 1

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

A REVISION OF MASSY'S CHECKLISTS OF 'SOUTH AFRICAN' CEPHALOPODA

By

Martina A. Roeleveld

South African Museum, Cape Town

[*MS accepted 11 July 1974*]

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INTRODUCTION

The works of A. L. Massy and G. C. Robson are important milestones in the knowledge of southern African cephalopods. Robson published four papers in 1924 on the Cephalopoda collected by Dr J. D. F. Gilchrist when conducting the South African Marine Survey from the S.S. *Pickle*, and a short additional paper in April 1925. In January 1925, apparently without seeing Robson's papers of 1924 (possibly due to a delay in publication), Massy published her first paper on cephalopods of this region and included a checklist of South African Cephalopoda (pages 204–206), but unfortunately followed Hoyle's (1886) definition of this area. Hoyle's 'South African Region' (1886: 217 and map) extends from about Hollam's Bird Island on the west coast of southern Africa to the Red Sea, and includes Madagascar, Mauritius, the Tristan and Prince Edward Island groups, and the Kerguelen and Heard Islands. Massy's checklist covers this same region, but the more modern conception of the southern African region includes the area south of 20°S (Day 1967: vii). For pelagic and oceanic species the area has arbitrarily been restricted here to 20° to 45°S and 10° to 40°E. This excludes all the island groups and much of the east African coast.

It was considered that a separation into regions of the cephalopods listed by Massy (1925) will be of some use in compiling future checklists and distribution maps. Since future authors will wish to check on the localities of the species listed, and on the validity of the separation, before quoting their distributions, all relevant published records are given, as far as they could be traced. These are presumably the records upon which Massy based her checklist, although this cannot be verified, as she gave no details. Where possible, original references were checked for exact localities, but in a few cases the original references were not available; for references quoted at second hand, the source is given in brackets. Within the zoogeographic regions, the species are presented in the order and with the names and comments given by Massy (in boldface type), including her sometimes inconsistent abbreviations of authors' names and linking of dual authors by '&', 'e.' and 'et'. The year of publication of the species and, where necessary, synonyms, have been added (in lightface type).

The species listed by Massy have been divided into two major groups: species that occur in the southern African region (modern concept—20° to 45°S and 10° to 40°E) and those that occur outside this region. The non-southern African species have been allocated to four zoogeographical regions: southeast

Atlantic, Southern Ocean (south of 45°S), central Indian Ocean and northwest Indian Ocean.

A third group of species, those recorded from the southern African region up to 1925 but not listed by Massy, is also included, so that a complete list of cephalopod species known from the southern African region up to 1925 is now available.

Finally, the taxonomic papers published by Robson (1926) and Massy (1927, 1928), and ending with Massy's list of additions to her checklist (1928: 89–90), are discussed. No attempt has been made to bring the checklist up to date beyond 1928, as new records still come to hand with sufficient frequency to show that the cephalopod fauna of this region is as yet incompletely known. Recent checklists have been published by Voss (1962, 1967) and Barnard (1974).

SOUTHERN AFRICAN SPECIES LISTED BY MASSY (1925)

***Gonatus fabricii* (Lichtenstein,** 1818)

Gonatus sp. Steenstrup, 1882: 149 (translation) — one specimen ex *Diomedea exulans*, a different form to the arctic species of *Gonatus*, and fragments, probably of the same species, from 40°S, 15°E.

According to Clarke (1966: 152), *G. fabricii* is 'a widely distributed species from the colder regions of the north Atlantic and north Pacific . . .' and 'is quite distinct from all other species except *G. antarcticus* which is often considered a southern variety of *G. fabricii*.' According to Voss (personal communication) *G. fabricii* is most likely a complex of species, and there appears to be more than one species in the Atlantic; until distinctions have been made, *G. fabricii* must serve as a catch-all category.

(?) ***Teleoteuthis caribæa* (Lesueur,** 1821) [= *Onykia carriboea* Lesueur, 1821]

Teleoteuthis caribaea: Pfeffer, 1912: 49 — one specimen from 28°40′S, 10°45′E, one from 35°45′S, 22°06′E and one from the Cape of Good Hope. Thiele, 1920: 444 — one juvenile from 28°46′S, 10°17′E.

According to Voss (personal communication), the genus *Onykia* is in a somewhat similar situation to that of *Gonatus*, i.e. that *O. carriboea* is a complex of species.

***Onychoteuthis banksi* (Leach,** 1817)

Onychoteuthis banksii: Pfeffer, 1912: 70 — three specimens from the Cape of Good Hope. Odhner, 1923: 7 — one specimen washed on board off Table Bay.

***Lycoteuthis diadema* (Chun,** 1900)

Thaumatolampas diadema: Chun, 1910: 59 — 1♀ in vertical net to 3 000 m from *Valdivia* Sta. 89, southern part of Benguela Current, 31°21′S, 15°01′E; 1♀ in vertical net to 1 500 m from *Valdivia* Sta. 118, west wind drift, 40°31′S, 15°06′E.

? *Lycoteuthis* sp. A Robson, 1924*b*: 2 — 1♀ in 324 fm (595 m) from *Pickle* Sta. 156, 30°00′S, 31°22′E.

***Asthenoteuthion planctonicum* Pfeffer,** 1912 [= *Lycoteuthis diadema* (Chun, 1900)]

'Enoploteuthid larvae' Chun, 1910: 106 — two larvae from *Valdivia* Sta. 91, southern part of Benguela Current (no latitude or longitude could be traced for this station); four larvae from *Valdivia* Sta. 102, Agulhas Bank, 34°31′S, 26°00′E. Pfeffer (1912: 770) thought that these larvae pertained to *A. planctonicum*.

***Pterygioteuthis giardi* Fischer,** 1896

Pterygioteuthis Giardi: Chun, 1910: 131 — one larva from *Valdivia* Sta. 117, southern region of Agulhas Current (the position of this station could not be traced).

***Octopodoteuthis* larvae (Chun,** 1910) [= *Octopoteuthis* sp.]

Octopodoteuthis larvae Chun, 1910: 144 — two larvae in vertical net to 1 800 m from *Valdivia* Sta. 102, Agulhas Current, 34°31′S, 26°00′E.

***Benthoteuthis megalops* Verrill,** 1885 [= *Bathyteuthis abyssicola* Hoyle, 1885]

Benthoteuthis megalops: Chun, 1910: 185 — one specimen in vertical net to 2 500 m from *Valdivia* Sta. 115, origin of Benguela Current, 36°23′S, 17°38′E. Thiele, 1920: 453 — one specimen in vertical net to 2 500 m from north of Prince Edward Island, 43°04′S, 36°22′E.

***Brachioteuthis riisei* (Steenstrup,** 1882)

Tracheloteuthis Riisei: Hoyle, 1905: 93 — one specimen from 34°40′S, 27°E.

***Stenoteuthis bartrami* (Lesueur,** 1821) [= *Ommastrephes bartrami* Lesueur, 1821]

Ommastrephes Bartramii: Gray, 1849: 62 — four specimens from Cape of Good Hope.
? *Stenoteuthis Bartrami:* Pfeffer, 1912: 465 — one specimen from 'Cap'.
Stenoteuthis bartrami: Thiele, 1920: 455 — one juvenile from 28°30′S, 38°13′E. Massy, 1925: 206 — one specimen, washed up on shore after a storm, Durban.
According to Tomlin (1923: 40) Orbigny recorded this species as taken by Dussumier at the Cape.

***Symplectoteuthis oualaniensis* (Lesson,** 1830)

Ommastrephes oualaniensis: Gray, 1849: 63 — one specimen from ? Cape of Good Hope.
Loligo oualaniensis: Tryon, 1879: p. ? — specimens from Cape of Good Hope (according to Gibbons 1888: 202; Smith 1903: 355; Voss 1962: 246)

***Liocranchia reinhardti* (Steenstrup,** 1856)

Liocranchia reinhardti a Robson, 1924*b*: 6 — 2♀, 1? in 220 fm (404 m) from *Pickle* Sta. 100, 30°00′S, 31°19′E.

The only previous record that could be found, possibly for this region, is given by Pfeffer (1912: 673) as 'Südatl. Ozean (Putze vend., Mus. Göttingen)'.

***Pyrgopsis zygæna* (Vér.)** [Vérany, 1851]

? *Pyrgopsis rhynchophorus* Rochebrune, 1884: 23 — specimen(s) from Agulhas Bank (according to Clarke 1966: 223).

? *Pyrgopsis pacifica:* Robson, 1924*b*: 5 — 1?♀ in 180 fm (330 m) (not 100 fm as stated by Robson) from *Pickle* Sta. 258, 29°52′S, 31°15′E.

The systematics of the genus *Pyrgopsis* are confused; six species have been named (*P. zygaena* (Vérany, 1851); *P. schneehageni* (Pfeffer, 1884); *P. rhynchophorus* Rochebrune, 1884; *P. pacifica* (Issel, 1908); *P. lemur* Berry, 1920 and *P. atlantica* Degner, 1925), which have been synonymized in various combinations by different authors. Pfeffer (1900: 193) synonymized *P. rhynchophorus* Rochebrune, 1884, *Loligopsis schnehageni* [*sic*] Pfeffer, 1884 (= *Pyrgopsis schneehageni* (Pfeffer, 1884)) and *Taonius richardi* Joubin, 1895 (= *Galiteuthis armata* Joubin, 1898, according to Clarke (1966: 238)) with *Zygaenopsis zygaena* (Vérany, 1851), and lists one of the localities as 'Südspitze Afrikas' (? Rochebrune's record).

Chun (1910: 354) synonymized all the species referable to *Pyrgopsis* with *Euzygaena* (= *Pyrgopsis*) *pacifica* (Issel, 1908). Pfeffer (1912: 656–664) kept all the species separate, but thought that *P. zygaena* (Vérany, 1851) is probably synonymous with *P. rhynchophorus* Rochebrune, 1884. Clarke (1966: 221–223) synonymized *P. zygaena* (Vérany, 1851) with *P. pacifica* (Issel, 1908), but retained the others as separate species.

Recent authors (Clarke 1966: 221; Young 1972: 82; Voss, personal communication) believe that at least some of the *Pyrgopsis* species are probably larval forms of *Leachia* and other closely related cranchiid genera. Young (1972: 80) has shown that this is true for at least one species, *Leachia dislocata* Young, 1972.

Hoyle (1886: 217) listed *P. rhynchophorus* Rochebrune, 1884 under the 'South African' region, but not *P. zygaena* (Vérany, 1851). Massy (1925: 204) listed only the latter, presumably because she considered these two species to be synonymous. In fact, prior to Robson's (1924*b*) records of *P. pacifica* (which Massy did not apparently see before compiling her list), Rochebrune's record from the Agulhas Bank is the only southern African record of *Pyrgopsis*.

***Leachia cyclura* Lesueur,** 1821

Leachia cyclura Lesueur, 1821: 90 — one specimen from ? 'Pacific Ocean, 37°S, 33°E'.

Loligopsis cyclura Orbigny, 1848: 322 — specimen(s) from Cape Agulhas.

Megalocranchia maxima **Pfeffer,** 1884

Megalocranchia maxima Pfeffer, 1884: 24 — one specimen from Cape of Good Hope. This same specimen was described as *Desmoteuthis maxima* (Pfeffer 1900: 192) and again as *Megalocranchia maxima* (Pfeffer 1912: 712). Hoyle (1886: 217) listed this species as *Taonius* (?) *maximus*.

Loligo reynaudi **d'Orb.** [Orbigny, 1845] [? = *Loligo vulgaris* Lamarck, 1798]

Loligo reynaudii: Orbigny, 1848: 315 — specimen(s) from Cape of Good Hope. Gray, 1849: 73 — one specimen from Cape of Good Hope. Hoyle, 1910: 263 — 3♂ from Angra Pequena (= Lüderitzbucht). Hoyle, 1912: 280 — 13♀, 1?♀, 13♂ and 1 damaged in 35 fm (64 m) from *Scotia* Sta. 480, 8 miles (13 km) N of Dassen Island. Thiele, 1920: 440 — one specimen from *Valdivia* Sta. 101, Algoa Bay, 33°51'S, 25°29'E. Massy, 1925: 207 — 1♂, 1♀ in 35–40 fm (64–73 m) from Cape Henderson and 1♀ from Durban.

Loligo indica **Pfeffer,** 1884 [= *Loligo duvaucelii* Orbigny, 1835]

Loligo indica: Robson, 1924*d*: 654 — 1♀ in 36 fm (66 m) from *Pickle* Sta. 167, Natal coast, 29°31'S, 31°24'E. Massy, 1925: 208 — 2♂, 3♀ from Durban; 1♂ from Natal coast.

Sepioteuthis loliginiformis **(Ruppell & Leuckart,** 1828)

Sepioteuthis loliginiformis: Martens, 1879: 727 — specimen(s) from Inhambane.

Sepioteuthis mauritiana **Quoy e. Gaimard,** 1832 [= *Sepioteuthis lessoniana* Lesson, 1830]

Sepioteuthis lessoniana Férussac et d'Orbigny (= *S. mauritiana* Quoy et Gaimard): Joubin, 1898: 26 — specimen(s) from the Cape.
Massy presumably had not seen Joubin's paper, since she listed *S. mauritiana* (? on the basis of Quoy & Gaimard's record from Mauritius) but not *S. lessoniana*, whilst Joubin had already synonymized the two species, of which *S. lessoniana* has priority.

Sepioteuthis major **Gray,** 1828 **(Insufficiently characterized)** [? = *Thysanoteuthis rhombus* (Troschel, 1857)]

Sepioteuthis major Gray, 1828: 3 — specimen(s) from Cape of Good Hope (according to Gray 1849: 83).

Sepia vermiculata **Quoy e. Gaimard,** 1832 = ***hierredda*** **Rang,** 1837 [= *Sepia officinalis vermiculata* Quoy & Gaimard, 1832, *non* = *Sepia officinalis hierredda* Rang, 1837]

Sepia vermiculata Quoy & Gaimard, 1832: 64 — specimen(s) from Cape of Good Hope (according to Gibbons 1888: 202; Bartsch 1915: 250; Smith 1903: 356, 1916: 20). Robson, 1924*b*: 12 — 1♂ in 38 fm (70 m) from *Pickle* Sta. 386, 29°25′S, 31°37′E; and 1♂ from Natal coast. These same specimens were later (Robson 1924*d*: 639) described as *Acanthosepion vermiculata*. Massy, 1925: 209 — 1♀ in 40 fm (73 m) from Cape Henderson; 1♂ from Natal coast; 1♀ from Congella, Durban; 1♂ from Durban; 1♀ in 135 fm (248 m) from Natal coast.

Sepia hierredda (*non* Rang): Orbigny, 1841: 268 — specimen(s) from Cape of Good Hope. Smith, 1916: 20 — mentions specimens in the British Museum from Port Elizabeth, Cape Colony, and Tongaat Beach, Natal. In the previous paragraph, however, he states his belief that *S. hierredda* is synonymous with *S. vermiculata*, as suggested by Orbigny.

Sepia jousseaumi Rochebrune, 1884: 117 — specimen(s) from Cape of Good Hope (according to Smith 1903: 356, 1916: 22; Bartsch 1915: 250; Adam 1941: 108).

Sepia Filliouxi: Joubin, 1898: 24 — 1♂ from the Cape.

***Sepia zanzibarica* Pfeffer,** 1884

Sepia zanzibarica: Smith, 1916: 21 — one shell from Tongaat, Natal. Tomlin, 1923: 40 — specimen(s) from Isipingo.

***Sepia acuminata* E. A. Smith,** 1916 **(shell only known)**

Sepia acuminata Smith, 1916: 21 — shells from Port Elizabeth and Tongaat Beach, Natal. One shell from Tongaat, mentioned by Smith as being different from the others, is *S. hieronis* (Robson, 1924). Robson, 1924*b*: 12 — 2♀ in 192 fm (352 m) (not 95 fm as stated by Robson) from *Pickle* Sta. 95, 29°52′S, 31°17′E.

Rhombosepion acuminata Robson, 1924*d*: 643 — 2♀ from *Pickle* Sta. 95 (as above) and 2♂ in 160 fm (294 m) from *Pickle* Sta. 103, 29°54′S, 31°15′E.

***Sepia papillata* Quoy e. Gaimard,** 1832

Sepia papillata Quoy & Gaimard, 1832: 61 — specimen(s) from Cape of Good Hope (according to Krauss 1848: 133; Smith 1916: 22). Massy, 1925: 211 — 1♂ from 16 miles (26 km) NE of Bird Island.

Sepia tuberculata (*non* Lamarck): Orbigny, 1848: pl. 17, figs 13–15 — ? specimen(s) from Cape of Good Hope. Steenstrup, 1875: 479 — 1♂, 1♀, from the Cape. Hoyle, 1910: 265 — 3♀ from Angra Pequena (Lüderitzbucht).

Spathidosepion tuberculatum Rochebrune, 1884: 94 — 1♂ without shell from Cape of Good Hope (according to Adam 1944: 226).

***Sepia natalensis* sp. nov.** [= *Sepia simoniana* Thiele, 1920]

Sepia tuberculata (*non* Lamarck): Gray, 1849: 101 — one shell from Cape of Good Hope.

Sepia papillata (*non* Quoy & Gaimard): Smith, 1916: 22 — shells from Port Elizabeth and Tongaat Beach, Natal.

Sepia simoniana Thiele, 1920: 436 — 3♂, 2♀ from Simons Bay; one shell from Olifant River mouth. Odhner, 1923: 7 — one specimen in 40 fm (73 m) from 10 miles (16 km) from Cape Barracouta.

Sepia natalensis Massy, 1925: 212 — 1♀ in 35–40 fm (64–73 m) from Cape Henderson; 2♀ from 16 miles (26 km) NE of Bird Island; 1♀ from Durban.

***Sepia insignis* E. A. Smith, 1916 (shell only known)**

Sepia insignis Smith, 1916: 25 — two shells from Tongaat Beach, Natal.

***Sepia* (*Doratosepion*) *australis* Quoy e Gaimard,** 1832

Sepia australis Quoy & Gaimard, 1832: 70 — specimen(s) from Agulhas Bank to 90 miles (145 km) from Cape Agulhas (according to Krauss 1848: 133; Smith 1916: 24). Hoyle, 1912: 281 — 1♀ in 35 fm (64 m) from 8 miles (13 km) N of Dassen Island. Smith, 1916: 24 — shell(s) from Port Elizabeth. Robson, 1924*b*: 11 — 1♀, 1?♂ in 117 fm (215 m) from *Pickle* Sta. 2, 33°03′S, 17°42′E; 6♂, 6♀ in 112 fm (206 m) from *Pickle* Sta. 7, 32°32′S, 17°42′E; 2♂, 8♀ in 100 fm (184 m) from *Pickle* Sta. 9, 32°37′S, 17°41′E; 3♂ in 68 fm (125 m) (not 67 fm as stated by Robson) from *Pickle* Sta. 20, 32°20′S, 17°55′E; 1♂, 2♀ in 85 fm (156 m) from *Pickle* Sta. 44, 33°20′S, 17°49′E; 2♀ in 121 fm (222 m) from *Pickle* Sta. 54, 33°09′S, 17°36′E. These specimens were later described as *Rhombosepion capense* (Robson 1924*d*: 641).

Sepia capensis: Orbigny, 1848: 278 — specimen(s) from Agulhas Bank. Krauss, 1848: 133 — one specimen from Kalk Bay. Thiele, 1920: 438 — one specimen from *Valdivia* Sta. 114, Simons Bay, 34°20′S, 18°36′E; one specimen from *Valdivia* Sta. 101, Algoa Bay, 33°51′S, 25°29′E; five specimens from *Valdivia* Sta. 105, Agulhas Bank, 35°29′S, 21°03′E; one specimen from *Valdivia* Sta. 106, Agulhas Bank, 35°27′S, 20°56′E.

Sepia (*Doratosepion*) *australis* Massy, 1925: 214 — 1♂ from 16 miles (26 km) NE of Bird Island.

Hoyle (1886: 217) listed this species for South Africa as *Sepia capensis.*

***Sepia* (*Doratosepion*) *burnupi* Hoyle,** 1904

Sepia burnupi Hoyle, 1904: 27 (*partim*) — two shells from Umkomaas, Natal. Smith, 1916: 23 — shells from Tongaat Beach, Natal.

***Sepia* (*Doratosepion*) *incerta* E. A. Smith,** 1916

Sepia burnupi Hoyle, 1904: 27 (*partim*) — two shells from Port Elizabeth.

Sepia incerta Smith, 1916: 23 — shells from Tongaat Beach, Natal.

Sepia (*Doratosepion*) *burnupi* (*non* Hoyle) Massy, 1925: 215 — 1♂ in 38 fm (70 m) from Cape Henderson; 1♂ from Natal coast.

Sepia (*Doratosepion*) *incerta* Massy, 1925: 219 — 2♀ from Cape Henderson.

***Sepia* (*Doratosepion*) *confusa* E. A. Smith,** 1916

Sepia burnupi Hoyle, 1904: 27 (*partim*) — one shell from Port Elizabeth.

Sepia confusa Smith, 1916: 24 — shell(s) from Tongaat Beach, Natal.

Robson, 1924*b*: 12 — 2♀ in 158 fm (290 m) from *Pickle* Sta. 102, 29°51′S, 31°16′E; 1♀ in 36 fm (66 m) from *Pickle* Sta. 167, 29°31′S, 31°24′E; 2♂ in 192 fm (352 m) from *Pickle* Sta. 95, 29°52′S, 31°17′E; 1♂ in 180 fm (330 m) from *Pickle* Sta. 107, 29°49′S, 31°18′E. These specimens were later described as *Doratosepion confusum* (Robson 1924*d*: 647).

Sepia (*Doratosepion*) *confusa* Massy, 1925: 221 — 1♂ from Natal coast. Anatomy of the 'tail' of the male specimens described by Robson (1924) and Massy (1925) was described (as *Doratosepion confusa*) by Massy & Robson (1923: 435) and Carleton & Robson (1924: 259).

***Hemisepius typicus* Steenstrup,** 1875 [= *Sepia* (*Hemisepius*) *typica* (Steenstrup, 1875)]

Hemisepius typicus Steenstrup, 1875: 468 — 1♀ from Table Bay. Hoyle, 1912: 281 — 2♀ in 8–10 fm (15–18 m) from Saldanha Bay. Chun, 1915: 411 — 1♂, 1♀ from *Valdivia* Sta. 100, St Francis Bay, 34°09′S, 24°59′E.

***Velodona togata* Chun,** 1915

Velodona togata var. *a* Robson, 1924*a*: 206 — 2♂ in 220 fm (404 m) from *Pickle* Sta. 99, 29°55′S, 31°21′E; 1♀ in 250 fm (459 m) from *Pickle* Sta. 396, 29°55′S, 31°22′E; 1♀ in 240 fm (440 m) from *Pickle* Sta. 162, 30°03′S, 31°12′E. These specimens were later described as *Velodona togata* var. *capensis* (Robson 1924*d*: 644).

Strictly speaking this species should be listed with the non-southern African species, as Massy had not seen Robson's papers when she compiled the checklist, and the only previous record of *V. togata* was from the East African coast (Chun 1915: 479); but it is felt that this would only add to the confusion already caused by the checklist itself.

***Polypus granulatus* (Lam.)** [Lamarck, 1798] [= *Octopus vulgaris* Cuvier, 1797]

Octopus granulatus: Hoyle, 1886: 80 — one young specimen in 10–20 fm (18–37 m) from Simons Bay, Cape of Good Hope.

Polypus granulatus: Thiele, 1915: 487 — 1♀ from Cape Town. Thiele, 1920: 436 — 1 juvenile from Simonstown. Massy, 1925: 222 —— 1♀ from Park Rynie; 1♀ from Indian Ocean; 1♀ from Tongaat Beach, Natal; one mutilated specimen from H. Reich's coll.; 1♂ from 16 miles (26 km) NE of Bird Island; 1♀, 1♂ from Scottburgh, Natal; 1♂ from Durban.

Polypus rugosus: Robson, 1924*d*: 669 — 2♀ in 38 fm (70 m) from *Pickle* Sta. 388, Natal coast, 29°27′S, 31°37′E; 1♂ in 40 fm (73 m) from *Pickle* Sta. 389, Natal coast, 29°27′S, 31°39′E.

Robson (1929: 63) and Pickford (1955: 152) have placed *Octopus granulatus* Lamarck, 1798 in synonymy with *Octopus rugosus* (Bosc, 1792). Massy (1925: 222) was of the same opinion, as she listed *Polypus rugosus* (Orbigny, 1835) as a synonym of *Polypus granulatus* (Lamarck, 1798). She did not, however, recognize Bosc's inadequate description of *Sepia rugosa* (1792) as valid, and so upheld *Octopus granulatus* Lamarck as having priority, but at the same time giving priority to *Polypus* over *Octopus*. The priorities of these generic names are discussed by Robson (1929: 56), and Pickford (1955: 151) has discussed the complexities of the synonymies of *Octopus vulgaris*, *O. rugosus* and *O. granulatus*. On re-examining Robson's specimens Pickford (1955: 158) found that 'The majority of specimens from the eastern, western, central and south Atlantic, and from West and South Africa which Robson referred to this species (i.e. *O. rugosus*) are probably correctly assigned to *O. vulgaris*. It cannot be established that *O. rugosus* is a valid species.'

***Polypus horridus* (d'Orb.)** [Orbigny, 1826] [= *Octopus horridus* Orbigny, 1826]

Octopus argus Krauss, 1848: 132 — one specimen from Natal.

Octopus horridus: Gibbons, 1888: 201 — specimen(s) from Algoa Bay.

***Polypus valdiviæ* Chun,** 1915 [= *Bathypolypus valdiviae* (Thiele, 1915)]

? *Octopus capensis* Eydoux & Souleyet, 1852: 11 — one juvenile from Cape of Good Hope, insufficiently described. Thiele (1915: 485) and Robson (1932: 303) believed that this was probably identical with *Bathypolypus valdiviae*.

Polypus valdiviae Thiele, 1915: 485 — 1♂, 3♀ in 500 m from *Valdivia* Sta. 103, Agulhas Bank, 35°11′S, 23°02′E.

Bathypolypus grimpei Robson, 1924*a*: 208 — 1♂ in 470 fm (862 m) from *Pickle* Sta. 405, Natal coast, 30°00′S, 31°35′E; 3♂, 4♀ in 380 fm (697 m) from *Pickle* Sta. 164, Natal coast, 30°06′S, 31°31′E. Robson later decided (1932: 303) that the differences between *B. valdiviae* and *B. grimpei* were insufficient to warrant the erection of a new species for the latter.

Bathypolypus ? *valdiviæ:* Robson, 1924*d*: 669 — 1♂ in 220 fm (404 m) from *Pickle* Sta. 63, Cape Town, 33°42′S, 17°36′E.

'Undetermined polypods' Robson, 1924*d*: 670 — one specimen in 260 fm (477 m) from *Pickle* Sta. 46, west of Cape Town, 33°25′S, 17°24′E; one specimen in 260 fm (477 m) from *Pickle* Sta. 294 (?), 25°48′S, 33°38′E. Robson (1932: 303) placed these under *B. valdiviae*.

***Polypus capensis* (Eydoux et Souleyet,** 1852) [? = *Bathypolypus valdiviae* (Thiele, 1915)]

Octopus capensis Eydoux & Souleyet, 1852: 11 — one juvenile from Cape of Good Hope, insufficiently described.

***Polypus fontanianus* (d'Orb.)** [Orbigny, 1835] [= *Octopus fontanianus* Orbigny, 1835]

Polypus fontanianus: Massy, 1925: 224 — 1♀ from Natal coast. Robson (1929: 187) erected the genus *Joubinia* for this species and *Polypus campbelli*. He thought (1929: 189) that Massy's specimens represented a well-marked local variety, and named them *Joubinia fontaniana* var. *africana*. Adam (1938: 223) substituted *Robsonella* for *Joubinia*, as the latter was shown to be preoccupied. Pickford (1955: 163) re-examined Robson's specimens of *Robsonella fontaniana* and concluded that the genus *Robsonella* is probably not valid, and that the species assigned to it should be returned to the genus *Octopus*.

Cistopus indicus **Rapp,** MS [= *Cistopus indicus* (Orbigny, 1840)]

Octopus Indicus: Martens, 1879: 727 — specimen(s) from Inhambane, Moçambique.

Argonauta argo **Linn.** [Linnaeus, 1758]

Argonauta argo: Orbigny, 1840: 158 — Rang (1829) collected this species on the Agulhas Bank, and Reynaud in False Bay (no reference to Reynaud given). Krauss, 1848: 133 — shells in fairly large numbers on south coast of Cape Colony, from False Bay to Algoa Bay. Hoyle, 1886: 69 — one shell from Cape of Good Hope. Gibbons, 1888: 201 — specimen(s) from East London. Sowerby, 1892: 1 — this species is frequently found on the shores of South Africa. Bartsch, 1915: 2 — one specimen from Port Alfred.

Argonauta tuberculata **Shaw,** 1791 [= *Argonauta nodosa* Solander, 1786]

Argonauta nodosa: Humphrey, 1797: 6 — specimen(s) from Cape of Good Hope (according to Smith 1903: 355).

Argonauta tuberculata: Orbigny, 1826: 138 — specimen(s) from Cape of Good Hope (according to Robson 1932: 200). Krauss, 1848: 133 — Rang found this species at Cape Agulhas (no reference to Rang given).

[?] ***Argonauta böttgeri*** **Maltzan,** 1881

Sowerby (1892: 1) lists this species for South Africa and refers to his earlier paper (1889) where, however, *A. boettgeri* is not mentioned! Bartsch (1915: 230) also lists this species for South Africa, but gives no locality.

Amphitretus pelagicus **Hoyle,** 1885

Amphitretus pelagicus: Thiele, 1915: 532 — one specimen in vertical net to 1 800 m from *Valdivia* Sta. 102, Agulhas Current, 34°31′S, 26°00′E.

NON-SOUTHERN AFRICAN SPECIES LISTED BY MASSY (1925)

SOUTHEAST ATLANTIC

Hensenioteuthis melancholicus **(Chun,** 1906) [= *Sandalops melancholicus* Chun, 1906]

Sandalops melancholicus: Chun, 1910: 379 — two specimens in vertical net to 1 000 m from NE of Tristan da Cunha. The position was 32°08′S, 8°28′W (Thiele 1920: 458).

***Polypus verrucosus* (Hoyle,** 1885) [= *Octopus vulgaris* Cuvier, 1797]

Octopus verrucosus Hoyle, 1885: 222 — 2♂ from Inaccessible Island, Tristan da Cunha (according to Hoyle 1886: 79).

SOUTHERN OCEAN (SOUTH OF 45°S)

***Polypus levis* (Hoyle,** 1885) [= *Benthoctopus levis* (Hoyle, 1885)]

Octopus levis Hoyle, 1885: 229 — 2♂, 2♀ in 75 fm (137 m) from *Challenger* Sta. 151, off Heard Island, 52°59′30″S, 73°33′30″W (this should be 73°33′30″E) (according to Hoyle 1886: 98).

Thiele's (1915: 486; 1920: 435) specimen from Kerguelen was considered by Robson (1932: 227, 233) to be a distinct species, *Benthoctopus thielei.*

CENTRAL INDIAN OCEAN

***Architeuthis sancti-pauli* (Vélain,** 1877)

Mouchezia sancti-pauli Vélain, 1877: 83 — one specimen from St Paul Island.

Clarke (1966: 98) has since recorded specimens of *Architeuthis* spp. from the stomachs of sperm whales caught near Durban and Saldanha Bay.

***Enoploteuthis hoylei* Pfeffer,** 1884 [= *Abraliopsis hoylei* (Pfeffer, 1884)]

Enoploteuthis hoylei Pfeffer, 1884: 17 — 1♂ from the Mascarenes.

***Loligo tricarinata* Gray,** 1849 **(Insufficiently characterized)**

Loligo tricarinata Gray, 1849: 73 — two shells from Isle of France (Mauritius).

***Sepioteuthis madagascarensis* Gray,** 1849 **(Insufficiently characterized)**

Sepioteuthis madagascariensis Gray, 1849: 80 — one specimen from Madagascar.

***Sepiola stenodactyla* Grant,** 1833 [= *Euprymna stenodactyla* (Grant, 1833)]

Sepiola stenodactyla Grant, 1833: 84 — one specimen from Mauritius.

***Polypus aranea* (d'Orb.)** [Orbigny, 1826] [= *Octopus filamentosus* Blainville, 1826]

Octopus filamentosus Blainville, 1826: 188 — specimen(s) from Mauritius (according to Robson 1929: 143).

Octopus aranea: Orbigny, 1840: 57 — specimen(s) from Mauritius. Martens, 1879: 727 — specimen(s) from Moçambique.

NORTHWEST INDIAN OCEAN

***Abraliopsis morisii* (Vér.)** [Vérany, 1837]

Abraliopsis Morisii: Chun, 1910: 78 — 1♂ in 977 m from *Valdivia* Sta. 254, Indian North Equatorial Current, 0°29′S, 42°47′E; 1♀ in 1 134 m from

Valdivia Sta. 256, Indian North Equatorial Current, 1°49′N, 45°29′E; specimen(s) from stomach of *Coloconger raniceps* caught in 628 m from *Valdivia* Sta. 265, Indian North Equatorial Current, 6°24′N, 49°31′E.
According to Voss (personal communication) Chun's detailed illustrations involve probably three nominal species, *A. hoylei*, *A. lineata* and a new species (Voss, in manuscript).

Calliteuthis hoylei **(Goodrich,** 1896)

Calliteuthis Hoylei: Chun, 1910: 170 — 1♀ in vertical net to 2 000 m from *Valdivia* Sta. 235, Indian South Equatorial Current near Amirante Islands, 4°34′S, 53°42′E.
N. Voss (1969: 784) considered Chun's specimen to pertain to *Histioteuthis dofleini* (Pfeffer, 1912) and not to *Histiopsis Hoylei* Goodrich, 1896, a *species dubia.*

Mastigoteuthis glaucopis **Chun,** 1908

Mastigoteuthis glaukopis Chun, 1908: 88 — one specimen from proximity of East African coast. Chun, 1910: 233 — one specimen in 1 213 m from *Valdivia* Sta. 261, Indian North Equatorial Current, 4°63′S, 48°37′E (probably the same specimen).

Liocranchia valdiviæ **Chun,** 1906

Liocranchia Valdiviae: Chun, 1910: 337 — 1♀ in vertical net to 2 000 m from *Valdivia* Sta. 237, tongue of Indian South Equatorial Current, 4°45′S, 48°58′E; 1♂ in vertical net to 2 500 m from *Valdivia* Sta. 239, tongue of Indian South Equatorial Current, 5°42′S, 43°36′E; 1♂ in 1 362 m from *Valdivia* Sta. 258, Indian North Equatorial Current, 2°58′N, 46°50′E.

Corynomma speculator **Chun,** 1906

Corynomma speculator: Chun, 1910: 367 — one specimen in vertical net to 2 000 m from *Valdivia* Sta. 237, tongue of Indian South Equatorial Current, 4°45′S, 48°58′E.

Rossia mastigophora **Chun,** 1915

Rossia mastigophora Chun, 1915: 405 — 1♂, 2♀ in 638 m from *Valdivia* Sta. 253, Indian North Equatorial Current, 0°27′S, 42°47′E.

Sepia singalensis **Goodrich,** 1896 [= *Sepia pharaonis* Ehrenberg, 1831]

Sepia singalensis: Hoyle, 1907: 459 — 2♀ from Zanzibar.

Sepia venusta **Pfeffer,** 1884 [? = *Sepia pharaonis* Ehrenberg, 1831]

Sepia venusta Pfeffer, 1884: 12 — one specimen from Zanzibar.

Polypus horsti **(Joubin,** 1898) [= *Octopus cyanea* Gray, 1849]

Polypus horsti: Hoyle, 1907: 451 — four specimens from Zanzibar.

***Polypus herdmani* Hoyle,** 1904 [= *Octopus herdmani* (Hoyle, 1904)]

Polypus herdmani: Hoyle, 1907: 454 — 1♀, 1? in 10 fm (18 m), 1♀ in unknown depth, from Zanzibar.

***Polypus arborescens* Hoyle,** 1904 [= *Octopus arborescens* (Hoyle, 1904)]

Polypus arborescens: Hoyle, 1907: 454 — 1♀ in 5 fm (9 m), 4♀, 1♂ in 10 fm (18 m) from Zanzibar.

***Opisthoteuthis medusoides* Chun,** 1915 [= *Opisthoteuthis medusoides* Thiele, 1915]

Opisthoteuthis medusoides Thiele, 1915: 538 — two specimens in 400 m from *Valdivia* Sta. 243, Dar-es-Salaam, 6°39′S, 39°31′E.

O. medusoides is the only species of *Opisthoteuthis* that is bell-shaped, the others being more or less flat. In this connection Bidder (1968: 1038) has made an interesting comment: 'the "species" figured by Chun (1914) under the name "*medusoides*" should probably be regarded not as a true species, but as evidence of the medusa-like swimming . . . by some chance of fixation, a group of specimens were fixed in the "systole" of the swimming phase.' The swimming of cirrate octopods is also discussed by Roper & Brundage (1972). The author of *O. medusoides* was actually Thiele, who wrote part of Chun's *Valdivia* report, as stated on page 536 of that publication, and the year of publication was 1915, not 1914.

SPECIES LISTED IN ERROR

***Grimalditeuthis bonplandi* (Vér.)** [Vérany, 1837] [= *Grimalditeuthis bomplandi* (Vérany, 1837)]

Grimalditeuthis bonplandi: Pfeffer, 1900: 188 — lists this species as recorded from the southern tip of Africa, but according to Pfeffer (1912: 635) this locality is incorrect. According to Clarke (1966: 214) this species has been recorded from the North and Southwest Atlantic.

SOUTHERN AFRICAN SPECIES OMITTED BY MASSY (1925)

Although Massy apparently did not see Robson's papers (1924*a–d*), and certainly not that of 1925, which was published three months after her checklist, Robson's records are included here for completion of the checklist to 1925.

Moroteuthis sp. Robson, 1924

Moroteuthis sp.A Robson, 1924*b*: 2; 1924*d*: 595.
1♀ in 135 fm (247 m) from *Pickle* Sta. 530, 33°34′S, 17°23′E.

Abraliopsis gilchristi (Robson, 1924)

Abralia gilchristi Robson, 1924*b*: 3; 1924*d*: 601.
1♂ in 240 fm (439 m) from *Pickle* Sta. 48, 33°36′S, 19°30′E;
1♀ in 280 fm (512 m) from *Pickle* Sta. 81, 33°28′S, 17°19′E.

Octopodoteuthopsis sp. Robson, 1924

Octopodoteuthopsis sp. A Robson, 1924*b*: 4.
Octopodoteuthopsis sp. Robson, 1924*d*: 606.
One specimen in 900 fm (1 646 m) from *Pickle* Sta. 357 (not Sta. 347, as stated by Robson 1924*d*), 32°36′S, 16°00′E.

Histioteuthis bonnellii (Férussac, 1835)

Histioteuthis bonelliana: Robson, 1924*b*: 4; 1924*d*: 608.
1♀ in 470 fm (860 m) from *Pickle* Sta. 343, 30°10′S, 14°33′E;
1♂ in 958 fm* (1 752 m) from *Pickle* Sta. 542, 31°41′S, 17°09′E.
According to N. Voss (1969: 845), Robson's specimens pertain to *H. macrohista* N. Voss, 1969.

Todaropsis eblanae (Ball, 1841)

Todaropsis eblanae: Robson, 1924*b*: 5; 1924*d*: 614.
2♂, 3♀ in 112 fm (205 m) and 2♂ in 126 fm (230 m) from *Pickle* Sta. 7, 32°32′S, 17°42′E;
2♂, 7♀ in 100 fm (183 m) from *Pickle* Sta. 9, 32°37′S, 17°41′E;
1♂, 1♀ in 67 fm (123 m) from *Pickle* Sta. 20, 32°20′S, 17°55′E;
1♂ in 85 fm (155 m) from *Pickle* Sta. 44, 33°20′S, 17°49′E;
2♂, 1♀ in 67 fm (123 m) from *Pickle* Sta. 54, 33°09′S, 17°36′E;
1♂, 2♀ in 104 fm (190 m) (not 108 fm as stated by Robson 1924*b*) from *Pickle* Sta. 58, 32°26′S, 17°32′E.

Chiroteuthis sp. Robson, 1924

Cheiroteuthis (*Doratopsis*-stage) A Robson, 1924*c*: 591.
One larva in plankton net at 100 fm (183 m) off Durban, 29°55′S, 31°22′E.

Mastigoteuthis sp. Robson, 1924

Mastigoteuthis sp. A Robson, 1924*b*: 5; 1924*d*: 617.
One specimen in 820 fm (1 500 m) from *Pickle* Sta. 277, 29°42′S, 31°35′E.

Taonius pellucida (Chun, 1910)

Desmoteuthis pellucida Chun, 1910: 357 — 1♀ in vertical net to 1 000 m from *Valdivia* Sta. 90, Benguela Current, 33°20′S, 15°58′E.
Pfeffer (1912: 716) repeated the description of Chun's specimen under the name *Megalocranchia pellucida*.

Liocranchia intermedia Robson, 1924

Liocranchia intermedia Robson, 1924*b*: 6; 1924*d*: 632.
1♂ in 260 fm (475 m) from *Pickle* Sta. 174, Natal coast, 29°40′S, 31°41′E.

Cranchia scabra Leach, 1817

Cranchia scabra: Robson, 1924*b*: 10; 1924*d*: 624.
1 ?♀ in 820 fm (1 500 m) from *Pickle* Sta. 277, Natal coast, 29°42′S, 31°35′E.

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* According to the station list (Gilchrist 1922: 47) the depth at this station was 580 fm (1 061 m).

Galiteuthis armata Joubin, 1898

Galiteuthis armata: Robson, 1924*b*: 8; 1924*d*: 627.
1 ?♀ in 900 fm (1 646 m) from *Pickle* Sta. 357, Cape Town, 32°36′S, 16°00′E.

Anomalocranchia impennis Robson, 1924

Anomalocranchia impennis Robson, 1924*b*: 9; 1924*d*: 628.
One specimen in 418 fm (764 m) from *Pickle* Sta. 540, Cape Town, 33°30′S, 17°12′E.

Euprymna sp. Hoyle, 1912

Euprymna sp. Hoyle, 1912: 280 — one young specimen in 8–10 fm (15–18 m) from *Scotia* Sta. 482, Saldanha Bay.

Heteroteuthis hawaiiensis dagamensis Robson, 1924

Heteroteuthis hawaiiensis Berry, var. *dagamensis* Robson, 1924*b*: 11; 1924*d*: 632.
1♀ in 350 fm (640 m) from *Pickle* Sta. 176, Natal coast, 29°43′S, 31°49′E;
1♀ in 610 fm (1 116 m) from *Pickle* Sta. 251, Cape Town, 33°43′S, 17°24′E.

Rossia enigmatica Robson, 1924

Semirossia sp. A Robson, 1924*b*: 10.
Rossia enigmatica Robson, 1924*d*: 635.
1♀ in 220 fm (402 m) from *Pickle* Sta. 63, Cape Town, 33°42′S, 17°36′E;
1♂ in 151 fm (276 m) from *Pickle* Sta. 6, Cape, 32°32′S, 17°18′E;
1 ?♀ in 260 fm (475 m) from *Pickle* Sta. 46, 33°25′S, 17°24′E.
In the second paper (Robson 1924*d*) only the first two specimens above were listed for *R. enigmatica*; the third specimen is mentioned at the end of the description as being in poor condition, but probably also pertaining to this species.
Rossia sp. Robson, 1925: 450.
2♀ from 'Cape area'. Voss (1962: 253) re-examined these specimens and considered them to be conspecific with *R. enigmatica*.

Sepia tuberculata Lamarck, 1798

Sepia tuberculata: Orbigny, 1848: 277 — specimen(s) from Cape of Good Hope.
Spathidosepion tuberculatum Rochebrune, 1884: 93 — 1♀ and 1 shell from Cape of Good Hope (according to Adam 1944: 226).
Spathidosepion papillatum (*non* Quoy & Gaimard) Rochebrune, 1884: p? — 1♀ from Port Dorey (according to Adam 1944: 226). This locality is probably incorrect (Adam, personal communication); *S. tuberculata* is endemic to South Africa.
Gray (1849: 101) lists *S. tuberculata* from the Cape of Good Hope, but apparently synonymizes *S. papillata* with it; the only specimen Gray had, one shell, pertains to *S. simoniana*, according to Adam & Rees (1966: 109).

According to Montfort (see Smith, 1916: 25) Lamarck's types were from the Cape of Good Hope.

Hoyle (1886: 217) listed this species from 'South Africa', but followed Orbigny in considering *S. papillata* to be a synonym. Massy recognized that the two species are distinct, but listed only *S. papillata*, although *S. tuberculata* had been recorded from South Africa.

Sepia hieronis (Robson, 1924)

Sepia acuminata Smith, 1916: 21 (*partim*) — one shell from Tongaat Beach, Natal.

Sepia sp. A Robson, 1924*b*: 13.

Rhombosepion hieronis Robson, 1924*d*: 645.

Two specimens in 117 fm (214 m) from *Pickle* Sta. 2, 33°03′S, 17°42′E;
2♀ in 112 fm (205 m) from *Pickle* Sta. 7, 32°32′S, 17°42′E;
1♂ in 126 fm (230 m) from *Pickle* Sta. 8, 32°33′S, 17°29′E;
one specimen in 150 fm (274 m) from *Pickle* Sta. 33, 32°54′S, 17°25′E.

Sepiella cyanea Robson, 1924

Sepiella cyanea Robson, 1924*b*: 13; 1924*d*: 648.

1♀ in 40 fm (73 m) (not 60 fm as stated by Robson 1924*d*) from *Pickle* Sta. 389, 29°27′S, 31°39′E;
1♂ in 28 fm (51 m) from *Pickle* Sta. 476, 29°17′S, 31°33′E.

Spirula spirula (Linnaeus, 1758)

Spirula peronii: Krauss, 1848: 134 — many shells found after storm on beach at Plettenberg Bay. Gibbons, 1888: 202 — specimens from Table Bay, Algoa Bay and Natal. Sowerby, 1892: 1 — occasionally found on beach, Port Elizabeth. Bartsch, 1915: 3 — one specimen from Port Alfred.

Spirula solandri: Bartsch, 1915: 251 — listed for South Africa, but no locality or reference given.

Octopus vulgaris Cuvier, 1797

Octopus vulgaris: Krauss, 1848: 132 — three specimens from Natal coast·

Polypus vulgaris: Thiele, 1920: 436 — one specimen from Simons Bay.

Octopus schultzei (Hoyle, 1910)

Polypus schultzei Hoyle, 1910: 261 — 1♂ from Angra Pequena (Lüderitzbucht).

Eledone nigra (Hoyle, 1910)

Moschites nigra Hoyle, 1910: 262 — 1♂, 6♀ from Angra Pequena (Lüderitzbucht).

Robson (1932: 279) placed this species in the genus *Pareledone*, but Voss (personal communication) has re-examined the type and other specimens in the Berlin Museum and found that the species is a typical eledonid belonging to the genus *Eledone* (of which *Moschites* is a synonym).

Benthoctopus berryi Robson, 1924

Benthoctopus berryi Robson 1924*d*: 658.

1♀ in 1 200 fm (2 195 m) from *Pickle* Sta. 524, SW Cape Town, 33°31′S, 16°39′E (according to the station list (Gilchrist 1922: 44) the depth at this station was 1 220 fm (2 232 m)).

Argonauta hians Solander, 1786

Argonauta kochiana: Bartsch, 1915: 230 — listed for South Africa, but no locality or reference given.

Eledonella pygmaea Verrill, 1884

Eledonella massyæ Robson, 1924*a*: 202; 1924*d*: 672.

1♀ in 1 014 fm (1 854 m) from *Pickle* Sta. 87, SW Cape Town, 33°55′S, 17°06′E.

Cirroteuthis gilchristi Robson, 1924

Cirroteuthis gilchristi Robson, 1924*a*: 204; 1924*d*: 677.

1♂ in 1 400 fm (2 560 m) from *Pickle* Sta. 526, SW Cape Town, 33°17′S, 16°24′E.

Grimpoteuthis spp. (Robson, 1924)

Cirroteuthis A Robson, 1924*d*: 680.

Three specimens in 1 000 fm (1 828 m) from *Pickle* Sta. 525, Cape Town, 33°28′S, 16°40′E.

Eight specimens in 1 400 fm (2 560 m) from *Pickle* Sta. 526, Cape Town, 33°17′S, 16°24′E.

Cirroteuthis B Robson, 1924*d*: 682.

One specimen in 790 fm (1 443 m) from *Pickle* Sta. 85, 33°46′S, 17°12′E.

Robson later (1932: 155, 156) placed these specimens in the genus *Grimpoteuthis.*

Loligo burnupi Smith [*species dubia*]

Bartsch (1915: 241) lists this species from Port Shepstone; it is not known to what species or reference this refers.

Sepia affinis Orbigny, 1826 [*species dubia*]

According to Smith (1916: 26), Montfort (1805) recorded this species from the Cape of Good Hope, but Smith comments that '*Sepia affinis*, d'Orbigny, is not a *Sepia*, but evidently belongs to the genus *Sepioteuthis*, and although said by d'Orbigny and others to be the same as *Sepioteuthis sepoidea* [*sic*] (Blainville, 1823), it is not likely to be identical considering the remoteness of the localities—West Indies and South Africa'.

SEQUEL TO THE 1925 CHECKLIST

In 1926 Robson published a short additional paper on decapod cephalopods collected by the S.S. *Pickle*, including two species not covered in his previous papers on the collection, and constituting new records for southern Africa: *Tetronychoteuthis* sp. and *Histioteuthis bonnellii.*

The following year Massy (1927) described a collection of South African Cephalopoda made by the S.S. *Pieter Faure*. This collection included two new species, *Rhombosepion robsoni* (= *Sepia robsoni*) and *Sepia* (*Doratosepion*) *joubini*, and one new record, *Inioteuthis japonica* (? = *Inioteuthis capensis* Voss, 1962); the remaining species had already been recorded from southern Africa (1925 checklist and/or Robson 1924*a*,*b*,*d*).

In 1928 Massy described another collection of South African cephalopods, all but one of which had already been recorded from the region (checklist 1925). The remaining species was *Sepiella obtusata* (= *S. cyanea*, already recorded from South Africa by Robson 1924*b*,*d*). She also gave a list of additions to the checklist of 1925, consisting of the species described by Robson (1924*a*,*b*,*d*), but omitting *Sepiella cyanea*. She did not, however, include in this list of additions her own species and record described in 1927, nor did she mention the species described by Robson (1924*c*, 1926).

The additions to the checklist (for which the necessary synonyms have already been given) listed by Massy (1928) are as follows:

Moroteuthis sp. Robson, 1924
Lycoteuthis sp. Robson, 1924
Abralia gilchristi Robson, 1924
Octopodoteuthopsis sp. Robson, 1924
Histioteuthis bonelliana (Férussac, 1835)
Todaropsis eblanae Ball, 1841
Mastigoteuthis sp. Robson, 1924
Liocranchia reinhardti Steenstrup, 1856, var. Robson, 1924
Liocranchia intermedia Robson, 1924
Cranchia scabra Leach, 1817
Pyrgopsis pacifica (Issel, 1908)
Galiteuthis armata Joubin, 1898
Anomalocranchia impennis Robson, 1924
Loligo spp. Robson, 1924
Heteroteuthis hawaiiensis (Berry, 1909), var. *dagamensis* Robson, 1924
Rossia enigmatica Robson, 1924
Rhombosepion hieronis Robson, 1924
Velodona togata Chun, 1915, var. *capensis* Robson, 1924
Benthoctopus berryi Robson, 1924
Bathypolypus grimpei Robson, 1924
Cirroteuthis gilchristi Robson, 1924
Cirroteuthis sp. Robson, 1924
Eledonella massyae Robson, 1924

The species omitted by Massy (1928) but recorded from southern Africa up to 1928 are:

Cheiroteuthis sp. Robson, 1926 (= *Chiroteuthis* sp.)
Histioteuthis bonelliana (Férussac, 1835) (ex Robson 1926) (= *H. bonnellii*)

Tetronychoteuthis sp. Robson, 1926
Inioteuthis japonica Verrill, 1881 (ex Massy 1927) (? = *I. capensis* Voss, 1962)
Sepia (*Doratosepion*) *joubini* Massy, 1927
Rhombosepion robsoni Massy, 1927 (= *Sepia robsoni* (Massy, 1927))
Sepiella cyanea Robson, 1924

SUMMARY

Since Massy's checklist of South African Cephalopoda covers a very much larger area than that now considered to be the southern African zoogeographical region, the species listed by Massy have been separated into South African and non-South African. The locality records upon which Massy's checklist was probably based are given. For completion the species recorded from the southern African region up to 1925 but not listed by Massy (1925) are also given. Finally, the works of Massy and Robson on South African cephalopods, published up to 1928 and culminating in Massy's list of additions to the 1925 checklist, are briefly discussed.

ACKNOWLEDGEMENTS

I should like to thank Drs N. A. H. Millard and M. A. Cluver, both of the South African Museum, for advice on the manuscript.

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ISBN 0 949940 64 x

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

ADDITIONS TO THE SOUTH AFRICAN SPECIES OF PHTHIRIINAE AND USIINAE (DIPTERA: BOMBYLIIDAE) WITH KEYS TO ALL THE KNOWN SPECIES

By

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(With 3 figures)

[*MS. accepted 19 July 1974*]

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INTRODUCTION

The acquisition of additional material by more intensive field work and collecting, on the part of the South African Museum since my revision of the South African Phthiriinae (Hesse 1938: 822–866), necessitates the descriptions of quite a number of new species, the recording of undescribed sexes of species described from one sex only, and the correction of observations made on inadequate material.

It is also to be noted that since my revision of this subfamily, in which the genera *Phthiria* Meigen, *Apolysis* Loew and *Oligodranes* Loew were accommodated, Hull (1973: 194, 212) has transferred the two genera *Apolysis* and *Oligodranes* to the subfamily Usiinae which was formerly primarily based on the genus *Usia* from the Mediterranean Region and North Africa. The former subfamily Phthiriinae of authors thus becomes restricted to the genus *Phthiria*.

DESCRIPTIONS

Subfamily **Phthiriinae** Becker

Genus *Phthiria* Meigen

Phthiria: Hesse, 1938: 824. Hull, 1973: 195–199.

Phthiria laeta Bezzi

Phthiria laeta Bezzi, 1921: 96. Hesse, 1938: 831, fig. 248a.

The acquisition of additional ♀♀ and the as yet undescribed ♂ of this species throws an entirely different light on the identity of the species and necessitates not only additional observations to facilitate its recognition, but

Ann. S. Afr. Mus. **66** (12), 1975: 257–308, 3 figs.

also the correction of a taxonomic error made in allocating to it a variety (*xerophila*) which actually belongs to an entirely different species.

The species, both ♂ and ♀, may be recognized as follows:

Body on the whole less humped and broader than in other species, mainly black in ♂, only narrowish hind margins of sternites pallid; broadish hind margins of tergites on sides in ♂ appearing greyish white, due to greyish white tomentum; knees in ♂ yellowish; following parts in ♀ very pale yellow or yellowish white: the broadish occipital margin behind eyes continuous on each side with a broadish streak on each side of frons, extending down entire genae (excepting only for a black spot or streak on each side of antennae), the entire buccal cavity, entire head below (except for a short, central, basal, abbreviated, dark streak), the shoulders, sides of thorax above, slightly more than basal half of scutellum, broad hind margins of tergites (broader on sides), entire pleurae (except for dark lower part of mesopleuron, dark spot on anterior lower part of pteropleuron, a dark spot on anterior upper part of sternopleuron, the black lower parts or halves of sterno- and hypopleurae, and some infusions around base of halteres), the very broad, or almost entire, hind margins of sternites, and the coxae; legs in ♀ slightly more ochreous yellow, only hinder parts of trochanters, extreme apices of tibiae, and apices of tarsal joints, or sometimes apical halves of latter, darkened.

Vestiture with the hairs relatively sparse, a little denser in ♂, entirely white in ♂, slightly more sericeous yellowish on head above, occiput above and thorax above anteriorly in ♀; sparse scaling, where present, silvery whitish in ♂, and yellowish or golden above in ♀.

Head with the anterior and genal part not tumidly prominent; antennal joint 1 very short, subequal to joint 2; joint 3 (cf. Hesse 1938, fig. 248a) spindle-shaped, in profile slightly broadened at about middle above and again below nearer apex, but not humped, its lower apical process slightly thicker and projecting slightly more than upper one, the two together forming an almost symmetrical bifid process; proboscis about 2–2,8 mm, more slender in ♂.

Scutellum markedly broad and transverse, more so than in most other species, broadly rounded behind, its width being a little more than twice its length.

Wings greyish hyaline, with yellowish brownish, brownish to reddish-brownish veins; knobs of halteres entirely pallid in ♀, darkened above in ♂.

Legs with the basal joint of hind tarsi only about or a little more than half length of hind tibiae.

Length of body: about 4–4,5 mm
Length of wing: about 4,5–5 mm

Distribution

Transvaal (♂ allotype from Johannesburg (Zumpt, 24 December 1950)); Natal.

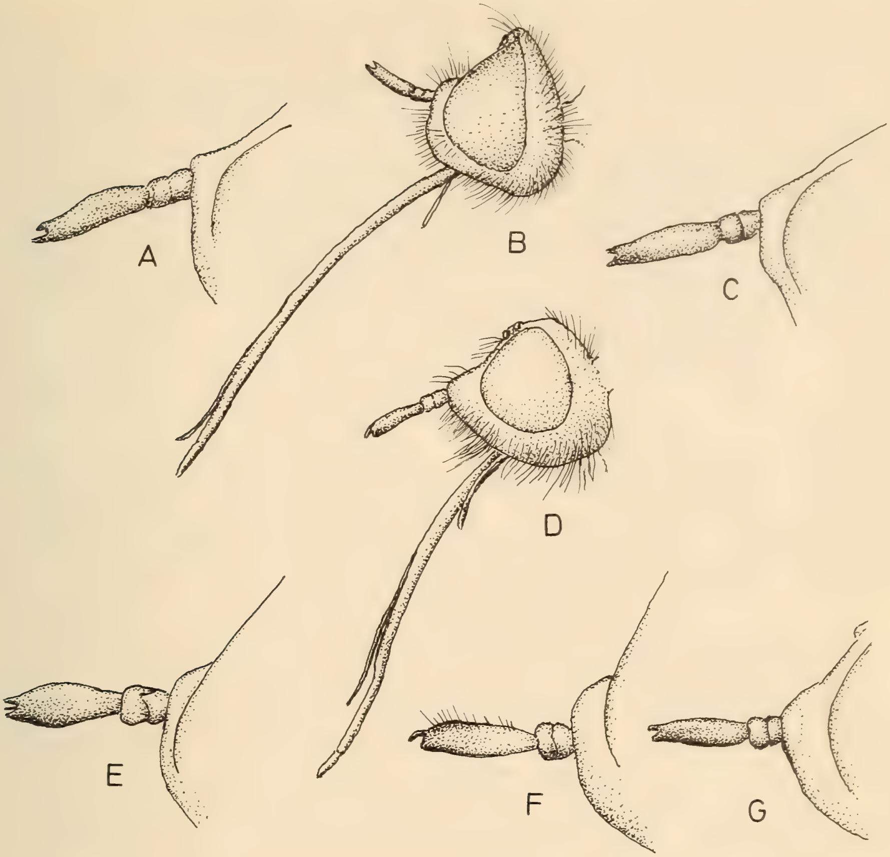

Fig. 1. Left side views of antennae and heads of some new species of *Phthiria.* (Antennae to the same scale, the heads to a smaller scale.)
A. ♀ *hesperia;* B. ♂ *nitidigena;* C. ♀ *flaviscuta;* D. ♀ *conocephala;* E. ♂ *ovalicornis;* F. ♂ *brunnescens;* G. ♀ *namaquensis.*

Phthiria flaviscuta sp. nov.

Fig. 1C

This species may almost be considered as only a distinct western Cape or southern Karoo variety of *laeta*. In the absence of the ♂ these ♀♀ are however placed as a separate species. Compared with the ♀ *laeta* they agree and differ in the following respects:

Body slightly smaller, with the same pattern of yellow, disposed in the same way, but the entire scutellum discally yellow and the yellow hind margins of tergites distinctly narrower, occupying less than apical halves of tergites on sides; legs with more darkened parts, the upper surfaces of front femora and sometimes a subapical infusion on inner or upper apical parts of the others, outer faces of all the tibiae, and the greater part of tarsi darkened. The left antenna is shown in Figure 1C.

Vestiture with the hairs and scaling, especially on thorax above and tergites, distinctly longer and denser, and distinctly more yellowish or golden; fine hairs and scaling on frons denser, more golden.

Wings very similar, but relatively shorter; knobs of halteres with a distinct dark spot above and tending to be darkened above in outer part.

The species appears to be slightly variable; some specimens have no lateral extension of the black on frons in front, and in others the legs are much darkened.

From 4 ♀♀ in the South African Museum.

Length of body: about 2,5–4 mm
Length of wing: about 3,5–4,5 mm

Distribution

Little Karoo: Oudtshoorn-Zebra (Museum expedition, October 1951) (holotype); Vanwyksdorp (October 1937); Spitskop near Meiringspoort (Museum staff, November 1935). South-western Cape: Franschhoek (Barnard, December 1932).

Phthiria hesperia sp. nov.

Fig. 1A

This species, represented by a ♀ specimen only, may eventually prove to be only a western form of *flaviscuta*, but in view of the absence of the ♂ and its distinct type of third antennal joint, it is referred to a separate species which differs from the ♀♀ of *laeta* and especially *flaviscuta* in the following respects:

Antennal joint 3 (cf. Fig. 1A) ending in an upper process which is much farther away from the apex, distinctly much more subapical in position and conspicuously less developed and thinner than the relatively stout lower apical process, but both these processes however more developed than in *laeta* and *flaviscuta*.

Central black fascia on frons not extending fascia-like laterally on frons in front as in *laeta*; yellow on sides of thorax anteriorly above as broad as in *flaviscuta* and broader than in *laeta*; entire scutellum yellowish as in former species; legs with the front femora and the other femora more extensively yellowish than in *flaviscuta*, and tibiae on the whole also more extensively yellowish, not so darkened on outer surfaces; hairs on legs apparently shorter and less developed than in *flaviscuta*; knobs of halteres without a distinct dark spot or infusion laterally above.

From a ♀ holotype in the South African Museum.

Length of body: 3,76 mm
Length of wing: about 3,88 mm
Length of proboscis: about 2 mm

Distribution

Western Cape: Leipoldtville (Museum expedition, November 1956).

Phthiria pulla Bezzi

Phthiria pulla Bezzi, 1922: 78. Hesse, 1938: 847.
Phthiria fallax Hesse, 1938: 836, fig. 250 (n. syn.).
Phthiria flavigenualis Hesse, 1938: 837, fig. 251 (n. syn.).
Phthiria laeta var. *xerophila* Hesse, 1938: 831, fig. 248b (n. syn.).

A long series of both ♂♂ and ♀♀ of a species of *Phthiria* from the Little Karoo and also the Great Karoo, obtained since the publication of my revision, has convinced me that the ♂♂ of the species in question are in fact the species *pulla* of Bezzi which he described from a ♂ specimen from Willowmore.

As I suspected in 1938 (p. 838) there is no doubt that my *flavigenualis*, described from 4 ♂♂, is identical with *pulla*. The single ♂ specimen, described as *fallax*, appears to be merely a colour variety and should also now be considered as a synonym of *pulla*.

The long series of ♀♀ in this collection obviously belong to the same species as the ♂♂ and constitute the as yet undescribed ♀ sex of *pulla*. Moreover the ♀♀ of my *laeta* var. *xerophila* also do not differ specifically from the above-mentioned newly-acquired ♀♀. In this case there is also no doubt that my *laeta* var. *xerophila* (both ♂ and ♀) represents a slight colour variety of *pulla*.

A more complete description of this slightly variable species *pulla*, as based on both sexes, is as follows:

Body in ♂ mainly black, only the narrow hind margins of sternites obscurely whitish or pallid, and last sternite infused with yellowish or reddish-yellow to a variable extent; body in ♀ with the following parts pale yellow to ochreous yellow: almost entire head (except the dark part on occiput surrounding the neck, the black ocellar region, an obscure dark central streak on frons of variable width and intensity to frontal depression, a dark spot on each side of antennae, the dark antennal joints 2 and 3, and the dark proboscis), broadish sides of thorax above, continuous anteriorly with a narrowish submedial dorsal line or streak on each side which often isolates a roundish dark humeral spot and another more transverse dark spot just above wing-bases, base of thorax to a variable extent, entire scutellum, greater part of pleurae (except the dark or black lower halves of sterno- and hypopleurae, the dark parts surrounding base of halteres, and usually some small obscure dark spots below wing-bases, and sometimes a darkish streak or infusion across lower part or half of mesopleuron), almost entire abdomen (except the dark or black bases of tergites, especially centrally and discally above), and the coxae; narrowish hind margins of tergites in ♀ tending to be more pallid or yellowish whitish, and the basal parts more orange or yellowish red; legs in ♂ black, but with rather conspicuous yellowish or reddish-yellow knees, with the entire femora, tibiae and bases of tarsi yellowish in one colour form (described by me as var. *xerophila*), and with only apices of femora, entire middle and hind tibiae, upper surfaces of front tibiae and bases of tarsi yellowish in another colour form (described as *fallax*); legs in ♀ entirely yellowish, only apices of tibiae and tarsi (or apical parts of tarsi) darkened.

Vestiture with the hairs and scaling relatively short and very sparse in typical ♀, but distinctly longer and denser, especially on abdomen of some ♀♀ (described as var. *xerophila*), the hairs in ♀ distinctly more yellowish, sericeous yellowish to pale golden on body above; vestiture on body and legs in ♂ much denser and longer than in ♀, entirely whitish or sericeous white, apparently denser in some ♂♂ with yellowish or partly yellowish legs (those described as var. *xerophila* and *fallax*); the ♂ more often with a greyish white tomentum or pruinescence which appears as broadish greyish white transverse band across hind margin on sides of tergites.

Head not tumidly prominent anteriorly; antennal joint 1 short, transverse, not longer than joint 2; joint 3 broadened at or near middle to a variable extent, subspindle-shaped, without any longish hairs above, its apical processes about equally long and prominent, the lower one a little broader at base, both together forming a more or less symmetrical bifid process; proboscis about 1,4–2,6 mm long, stouter in ♀.

Wings greyish hyaline, without a milky whitish tint; veins brownish to dark brown or even blackish-brown; middle cross vein at about, or a little beyond, middle of discoidal cell; knobs of halteres usually entirely pallid or pale yellowish above, but in some ♂♂ sometimes with a tendency to be slightly darkened on outer margin above.

Legs with the basal joint of hind tarsi usually longer or much longer than half length of hind tibiae.

Length of body: about 3–5 mm
Length of wing: about 3,5–5 mm

Distribution

Koup Karoo, Tankwa Karoo, Little Karoo, Great Karoo, and Namaqualand.

The synonymic names may be retained as varietal names for the various colour forms as indicated in brackets in the description above.

From the material before me it is evident that the typical *pulla* (syn. *flavigenualis*) occurs mostly in the Little Karoo and Great Karoo. The other colour form, *pulla* var. *fallax*, in which the ♂ has yellowish tibiae and the ♀ has denser hairs on the abdomen, appears to occur in the Koup Karoo and adjacent parts of the Great Karoo, extending into Namaqualand in the west where it is replaced by the variety *xerophila*, with entirely yellowish legs in the ♂. Still another, more southern, form of *pulla*, from the region between the Little Karoo and south Cape, may be added here:

Phthiria pulla var. ***anomalocera*** n.

The ♂ of this form differs from the ♂ of *pulla* Bezzi s.str. in being slightly smaller; antennal joint 1 distinctly longer, nearly twice length of small transverse joint 2; proboscis relatively shorter, only about 1,5 mm long; abdomen without distinct, or with less conspicuous, bands of greyish tomentum across hind margins of tergites on sides; last sternite entirely dark or black; and with the knobs of the halteres entirely very dark or black above.

From a ♂ in the South African Museum.

Distribution

South Cape: Uniondale District (Museum expedition, October 1952).

Phthiria varipes sp. nov.

This species obviously belongs to the South West African *crocogramma* and *cognata* section (Hesse 1938: 833, 835) in which the ♀♀ have very dark or black legs, less yellow on pleural parts, relatively narrower yellow hind margins across tergites, often rather broadish wings, and a third antennal joint in which the upper apical process is shorter, less developed and apparently farther back than lower one.

It is nearer *crocogramma* which type of species it represents in South Africa. Though having the yellow on its body disposed in the same way, it differs from the latter in the following respects:

Body distinctly smaller; entire occiput behind eyes in at least its upper half black, not with yellow eye margins; base of thorax entirely black like rest of thorax above; anterior spiracular part below humeral angle without any, or scarcely any, yellow; yellow hind margins of tergites distinctly narrower.

Head with the lower apical process of antennal joint 3, though longer, or projecting more, than upper one, not markedly stouter as in *crocogramma*; proboscis distinctly much more slender, much shorter, only about 2 mm long.

Wings more vitreous hyaline, without the faint, but distinct, subopacity of *crocogramma*.

Legs with the front coxae more yellowish-brown in front in apical part, not entirely black; femora not entirely or uniformly dark, but with more pale yellowish-brown on inner and upper faces in more than their basal halves, and the knees not so broadly yellowish.

From a ♀ holotype in the South African Museum.

Length of body: about 3 mm
Length of wing: about 4 mm

Distribution

Moordenaars Karoo, north-west of Laingsburg (Museum staff, March 1937).

Phthiria pubescens Bezzi

Phthiria pubescens Bezzi, 1921: 98. Bezzi, 1922: 77–78. Hesse, 1938: 839. (♀ only.)

In my revision of the South African species of *Phthiria* I refered a ♂ specimen from 'Weenen in Natal (Thomasset, March–April 1924)' to this species, at the same time ignoring an undescribed ♂ specimen referred to the same species by Bezzi and which was supposed to be in the Hungarian Museum, but which I could not identify from Bezzi's references and unsatisfactory key (Bezzi 1922: 77). This ♂ in any case no longer exists for the dipterous collections in that museum were destroyed by fire during the revolution of 1957.

Since the publication of my revision another ♂ and two ♀♀ from the same locality and obtained by the same collector as the above-mentioned ♂ have come to my notice. The differently coloured ♀♀, which obviously belong to the same species as the ♂, prove that my interpretation at the time was wrong and that the ♂ specimen described by me as the ♂ of *pubescens* is not the ♂ of that species. It, together with the other ♂ and the ♀♀, are described below as a new species.

The ♂ of *pubescens* Bezzi s.str. is therefore still unknown and this species is still represented only by the unique ♀ specimen, labelled by Bezzi, in the South African Museum.

Phthiria tinctipennis sp. nov.

Phthiria pubescens (♂ only) Hesse (nec Bezzi), 1938: 839, fig. 252 (n. syn.).

As mentioned under the preceding species, a ♂ specimen from Weenen in Natal was, in the absence of the true ♀, wrongly described by me as the ♂ *pubescens* Bezzi. It, together with another ♂ and 2 ♀♀ from the same locality and collected at more or less the same time by the same collector, as well as a slightly aberrant or varietal ♂ from the Transvaal, constitute a distinct and separate species which is characterized and differs from other known South African species as follows:

Body in ♂, including legs, mainly black, the legs sometimes however slightly more brownish or even yellowish brown, especially the front and middle ones; the following parts in ♀ very pale yellowish or ivory yellowish: sides of frons, genae, head below narrowly on sides along eye margin to about or nearly halfway up behind eyes in occipital part, sides of thorax above (except for a gap just above wing-bases), entire discal part of scutellum, propleural callosity above front coxae, a broadish pleural fascia along nearly upper half of sternopleuron across lower hinder part of pteropleuron up to base of halteres, metapleural part at same level, almost entire tergites 2 and 3, very broad hind margins of rest of tergites, and the very broad hind margins of sternites; buccal rim in ♀ dark or blackish; legs in ♀ almost entirely yellowish, only the tarsi, or at least their apical halves, darkened.

Vestiture with the hairs and scaling mainly whitish, longer and denser in ♂, more sericeous yellowish on abdomen above in ♀.

Head with the front part not tumidly prominent or swollen; antennal joint 1 very short, transverse, about as long as, or only very slightly longer than, 2; joint 3 not distinctly spindle-shaped, only a little narrowed apically and basally, with distinct bristly hairs above, its lower apical process quite prominent, even a little more prominent than upper one, the two together however forming a distinct bifid process; proboscis about 2–2,4 mm long.

Wings distinctly, though faintly, dusky, tinted yellowish brownish subapically to even brownish throughout, distinctly more so than in any other known South African species; veins yellowish-brown or reddish-brown; knobs of halteres darkened above, sometimes more so in ♀.

Hypopygium of ♂ as that figured in figure 252 (Hesse 1938: 840) erroneously referred as belonging to *pubescens* Bezzi.

From 3 ♂♂ and 2 ♀♀ (♂ holotype in British Museum (Natural History), ♀ allotype in South African Museum).

Length of body: about 3,5 mm
Length of wing: about 4–4,5 mm

Distribution

Natal: Weenen (Thomasset, March–April 1924) (♂ holotype, ♂ paratype, and ♀ paratype); Weenen (Thomasset, November 1928–March 1929) (♀ allotype). Transvaal: Potchefstroom (Zumpt, 26 December 1952) (♂ paratype).

From *crocogramma* Hesse, which it very closely resembles, it may at once be distinguished by the distinctly more dusky wings, relatively shorter discoidal cell, darkened halteral knobs, yellowish legs in ♀ and not distinctly yellowish knees in ♂, much shorter proboscis, more symmetrical bifid apex of antennal joint 3 in which the upper apical process is not so markedly subapical in position.

The ♀ which also superficially resembles *laeta* Bezzi, may at once be distinguished from the latter by the distinctly dusky wings, the distinctly narrower and less transverse scutellum and which is entirely yellow on disc, the narrower and more humped body, less extensive yellow on pleurae, etc.

Phthiria nitidigena sp. nov.

Fig. 1B

Body in ♂ entirely black; legs sometimes more dark sienna brownish to blackish-brown; integument of body, especially above and especially frons, genae, head below, thorax above, scutellum, and abdomen above, markedly or brilliantly shining, without any greyish white pruinescence.

Vestiture, as in most other ♂♂ of *Phthiria*, longish, but not very dense; hairs on ocellar tubercle, frons, and genae black or dark; short ones on abdomen above and longer ones on genital structures also dark; longer and sparser ones on abdomen above and on scutellum pale, slightly straw-coloured yellowish; rest of hairs on body and legs, especially denser ones on head below, sides of tergite 1 and on venter, more whitish; fine hairs or hair-like scaling on tibiae dark, and fine longish hairs on apical parts of femora also appearing dark in certain lights.

Head (cf Fig. 1B) with the front part rather protruding spout-like, the frons and genae broad, convex, tumid, much like those of *lanigera*, but to a lesser extent; antennal joint 1 short, transverse, not longer than 2; joint 3 more parallel-sided than in most other species, equally broad throughout, not humped or spindle-shaped, with some distinct fine hairs above, ending apically in a slightly longer lower process and a shorter upper process which is slightly farther back; palps apically slightly spear-blade-shaped; proboscis slender, about 2,4–2,7 mm long.

Wings very feebly greyish hyaline, without a very distinct subopacity, iridescent; veins pale yellowish brownish; middle cross vein a little beyond middle of discoidal cell; knobs of halteres entirely whitish.

Legs with the basal joint of hind tarsi distinctly much more than half length of hind tibiae.

From 3 ♂♂ in the South African Museum.

Length of body: about 4 mm
Length of wing: about 4,25–4,5 mm

Distribution

South-western Cape: between Leipoldtville and Elands Bay (Museum expedition, November 1948).

The markedly shining frons, genae, scutellum and upper parts of the body, spout-like anterior part of the head, dark hairs on frons and genae, and the parallel-sided third antennal joints easily distinguish this species from most of the known South African species.

Phthiria lanigera Bezzi

Phthiria lanigera Bezzi, 1921: 97. Hesse, 1938: 840, fig. 253.

This characteristic Cape species, which appears to be a montane species, is subject to variation and a distinct variety of it, described below, has since been taken together with the more typical form.

Phthiria lanigera var. ***melampogon*** n.

This variety differs from the typical form of *lanigera* in the following respects:

Vestiture with the hairs on frons, genae, and antennal joints 1 and 2 above in ♂ distinctly very much denser and longer, those on frons, antennae above, and upper part of genae black (those on frons and entire genae in typical ♂ distinctly less dense and entirely white); hairs on upper part of genae in ♀ also, very much denser, black, not white, and extreme upper part of genae on sides of antennae, though also black and shining, not entirely smooth as in *lanigera*, but with some black hairs; hairs and woolly scaling on body above in varietal ♀ paler yellowish sericeous or pale brassy yellowish, not so golden or deep golden yellowish.

Wings distinctly and more conspicuously milky whitish; veins also distinctly paler, more yellowish brown or yellowish, not brown or blackish brown; knobs of halteres in ♀ ivory whitish or yellowish above.

The varietal form also has antennal joint 3 relatively thinner or more slender basally, and the knees are either not, or scarcely, or at least less conspicuously, yellowish.

From 5 ♂♂ and 9 ♀♀, including the ♂ holotype and ♀ allotype, in the South African Museum.

Length of body: about 5,12–6,4 mm
Length of wing: about 5,4–5,52 mm

Distribution

South-western Cape: Wit River Valley in Bainskloof near Wellington (Museum expedition, December 1949) (♂ holotype, ♀ allotype, and paratypes); Wit River, Bainskloof (Barnard and Lawrence, November 1922); Wit River, Bainskloof (Barnard, November 1937) (♂ and ♀ paratypes).

Phthiria nigribarba Hesse

Phthiria nigribarba Hesse, 1938: 843, fig. 255.

Of this species, which I described from only 2 ♂♂ in 1938, the South African Museum has since obtained not only a number of other ♂♂, but also a series of the as yet undescribed ♀. Supplementary notes on the species and a description of the ♀ can now be added as follows:

Body entirely black in both sexes, appearing greyish white, especially markedly so in ♀, due to a conspicuous greyish white pruinescence; hind margins of sternites sometimes, even in ♂♂, very obscurely and narrowly pallid; basal part, or half, of palps yellowish in ♀ to yellowish brownish or sienna brownish in ♂; legs variable in colour, varying from entirely yellowish in some ♀♀ to yellowish tibiae and tarsi, and yellowish brown, brown, to sienna brownish femora in other ♀♀, and from entirely dark reddish or sienna brownish femora with yellowish knees in some ♂♂ to paler yellowish brown in others.

Vestiture with the hairs rather dense and long in both sexes, denser and shorter on body in ♀, on the whole much like those of *lanigera*; hairs in upper part of occiput, on ocellar tubercle, frons, and genae much denser and longer in ♂ and black, entirely sericeous white in ♀ like rest of hair on body and legs in both ♂ and ♀.

Head with the anterior part in ♂ tumidly prominent and swollen as in ♂ of *lanigera*; this part in ♀ less swollen, but with the upper part of genae and the frons nevertheless broader and more convex than in other species, excepting those in the *lanigera* section; antennal joint 1 short, subequal to, or scarcely longer than, 2; joint 3 spindle-shaped or humped, without distinct hairs above, its upper apical process distinctly longer than lower one, slightly curved, but relatively less stout than in *lanigera*; proboscis about 2–2,6 mm long, stouter and relatively shorter in ♀ than in ♂.

Wings conspicuously milky whitish in both sexes, with very pale yellowish or pallid, to almost white, veins; middle cross vein much beyond middle of discoidal cell; veins enclosing anal cell markedly straight; anal cell with its apical stalk relatively long in both sexes, usually longer than apical cross vein of discoidal cell; knobs of halteres entirely pallid or very pale in both sexes.

Length of body: about 3,5–5 mm
Length of wing: about 3,5–5 mm

Distribution

South-western Cape: Malmesbury (Brauns, October 1926) (type material); Klipheuwel near Cape Town (Zinn, October 1950) (♂♂ and ♀♀ and ♀ allotype).

Phthiria ovalicornis sp. nov.

Fig. 1E

A species very near *nigribarba* and also belonging to the *lanigera* section. It agrees with and differs from *nigribarba* in the following respects:

Body also entirely black in both sexes, also covered with a very conspicuous greyish white pruinescence in ♀; palps dark; legs much darker, even in ♀, blackish brown to black, sometimes more sienna brownish in ♀, only the knee-articulations sometimes reddish brown.

Vestiture very similar to that of *nigribarba*, but the hairs in ♀ distinctly denser than in ♀♀ of latter; dark hairs on ocellar tubercle, frons and genae in ♂ distinctly less dense and shorter, and in ♀ much sparser and shorter in this species, but also entirely sericeous white, like rest of hair on body and legs, in both sexes; hairs in occiput in ♂ also whitish, not dark as in ♂ of *nigribarba*.

Head in ♂ in front, especially genal parts, very similar to that of *nigribarba* and *lanigera*, but somewhat less tumidly prominent, less evident in ♀ where the genae are much shorter than in *nigribarba*, though the frons is broader, more convex than in ♀♀ of most species of *Phthiria*; antennal joint 1 (cf. Fig. 1E) also short, not visibly longer than 2, sometimes tending to be even shorter; joint 3 (cf. Fig. 1E) relatively shorter, characteristically oval or spindle-shaped, broadest at about, or just before, middle, slightly hollowed or depressed on inner side from just before middle and with some fine hairs above, more distinct in ♂, the upper apical process of joint relatively shorter than in *nigribarba*, but nevertheless stouter and slightly longer than lower one; palps relatively shorter, less projecting; proboscis 1,8–2,4 mm long.

Wings also conspicuously milky whitish, with yellowish veins which are however sometimes less pallid or whitish; second submarginal cell markedly acute basally, more so than in any other of the known South African species; middle cross vein much beyond middle of discoidal cell; knobs of halteres entirely pallid or whitish, but in some ♂♂ tending to be darker above.

Legs with the basal joint of hind tarsi distinctly very much longer than half length of hind tibiae, much more so than in *nigribarba*.

From 12 ♂♂ and 12 ♀♀ (♂ holotype, ♀ allotype and ♂ and ♀ paratypes) in the South African Museum.

Length of body: about 3,5–4,5 mm
Length of wing: about 4–4,5 mm

Distribution

North-western Karoo: Augusfontein near Calvinia (Museum expedition, September 1947).

Phthiria brunnescens sp. nov.

Fig. 1F

Another species in the *lanigera* section characterized as follows:

Body in ♂ entirely black; legs very dark blackish brown or dark sienna brownish, only the knee-articulations paler, more yellowish brown.

Vestiture with the hairs dense in ♂, but rather short, differing from ♂♂ of all other known South African species in having not only the hairs on head and occiput entirely black, but also dark ones intermixed on thorax above and on scutellum, short dark hairs on abdomen above, and blackish brown or dark ones on coxae and legs; the paler hairs on thorax above, to a certain extent on pleurae, and on sides of abdomen beyond tergite 1 gleaming more yellowish to pale yellowish brownish; with even the more whitish ones on mesopleuron, sides of tergite 1, and on venter gleaming more sericeous yellowish in certain lights.

Head with the frons and genae slightly tumidly prominent or inflated, placing the species at once into the *lanigera* and *nigribarba* section; antennal joint 1 short, subequal to, or only very slightly longer than, joint 2; joint 3 (cf. Fig. 1F) humped as in the *lanigera* section, but slightly beyond the middle, with distinct and conspicuous hairs above, ending apically in a slightly curved process, slightly longer and stouter than lower process; proboscis about 2 mm long; palps rather long, longer than antennae.

Wings greyish hyaline, with a slight subopacity, but not conspicuously milky whitish as in the *lanigera* section; veins yellowish brown; middle cross vein at about, or only a little beyond, middle of discoidal cell; knobs of halteres darkened above.

Legs with the basal joint of hind tarsi distinctly much more than half length of hind tibiae.

From a ♂ specimen in the South African Museum.

Length of body: about 4 mm
Length of wing: about 4 mm

Distribution

South-western Cape: Citrusdal District (Museum expedition, November 1948).

Phthiria namaquensis sp. nov.

Fig. 1G

A species which is also referable to the *lanigera* section on account of the structure of its third antennal joint and its milky whitish wings, but in which the head in front is not markedly inflated or tumidly prominent. It is characterized as follows:

Body and legs black in ♂ and also mainly so in ♀; the following parts in ♀ pallid or yellowish: a short transverse streak on each side in frontal depression, more or less lower half of genae, continued as a narrow streak along margin of eyes on head below and halfway up behind eyes in occipital part, the small boss-like prominence in middle of pleurae between sterno- and hypopleurae and pteropleuron and sometimes to a certain extent even adjacent parts of sterno- and metapleurae, and very narrow hind margins of sternites; knees in both sexes pallid or yellowish; integument of head and body in both sexes densely covered with greyish white bloom, on thorax above in longitudinal streaks and on abdomen above, especially in ♂, as greyish white rings across hind margins of tergites.

Vestiture with the hairs fairly dense, more so and longer in ♂, but relatively less so than in other species of this section, entirely sericeous whitish, but in ♂ with some hairs in occiput above behind eyes, those on ocellar tubercle and frons dark and, in ♀, also with some hairs on frons in front dark.

Head with the anterior part in ♂ not so obviously tumid as in *nigribarba* or even *brunnescens*, but with the frons and upper part of genae, even in ♀, slightly broader or more convex than normally so; antennal joint 1 very short, transverse, subequal to joint 2; joint 3 (cf. Fig. 1G) more or less subparallel-sided, not distinctly humped, without distinct hairs above, its upper apical process slightly, but distinctly, longer and stouter than the conspicuous lower one; proboscis about 1,6–2,2 mm long, not very much stouter in ♀ than in ♂.

Wings with a distinct milky whitish tint; veins brownish or dark brown; middle cross vein a little beyond middle of discoidal cell; apical stalk of anal cell, especially in ♀, tending to be shorter than in most other species; knobs of halteres, even in ♀, darkened above to a variable extent.

From 4 ♂♂ and 4 ♀♀, including the types, in the South African Museum.

Length of body: about 3–4 mm
Length of wing: about 3,5–4 mm

Distribution

Namaqualand: Papendorp (Museum expedition, October 1950) (♂ holotype and ♀ allotype); Wallekraal (Museum expedition, October 1950) (3 ♂ and 3 ♀ paratypes).

Phthiria conocephala sp. nov.

Fig. 1D

A species also belonging to the *lanigera* section as far as the shape of the third antennal joint, the milky whitish tinted wings and rather dense vestiture are concerned, but the front part of head is very similar to that of *pilirostris*

It is characterized as follows:

Body and legs in ♀ mainly black; a narrowish streak on each side of frons, more than lower half of genae, entire head below, excepting only a central dark streak, pale yellow, this pale yellow also continued as a narrow streak behind eyes, halfway up occiput and then continued as hind margin of eye itself, as a propleural spot above front coxae, a spot next to it just behind base of anterior coxae, a streak along middle of pleurae from posterior upper part of sternopleuron, lower part of pteropleuron, across upper part of hypopleuron, metapleural part in front of and just below halteres, and to a lesser extent also upper anterior angle of pteropleuron below wing-base; small area below wing-base ferruginous.

Vestiture with the hairs and scaling relatively dense and long, especially on genae, head below, on abdomen, and on femora, predominantly sericeous or silvery whitish, but those on front part of frons and upper parts of genae dark or black.

Head (cf. Fig. 1D) front markedly conically produced and narrowed apically, more so than in ♀♀ of *lanigera* and *nigribarba* section, more like that of ♀ *pilirostris*; buccal cavity sloping backwards; antennal joint 1 a little, but distinctly, longer than 2, about 1¼ times length of 2; joint 3 not very distinctly humped, only slightly broadened beyond middle, without distinct hairs above, its upper apical process stouter and longer than the lower feeble prominence, slightly curved down; proboscis about 2,2 mm long.

Wings distinctly tinted milky whitish; veins brownish or yellowish brown; middle cross vein much beyond middle of discoidal cell; apical stalk of anal cell rather long, very slightly longer than apical vein of discoidal cell; squamae conspicuously pallid or yellowish white; knobs of halteres with a small dark spot basally above.

Legs with the basal joint of hind tarsi only about half length of hind tibiae.

From a single ♀ specimen in the South African Museum.

Length of body: about 4,4 mm
Length of wing: about 4,2 mm

Distribution

Coastal part of western Cape: Graafwater (Museum expedition, October 1947).

REVISED DESCRIPTIVE KEY TO THE KNOWN SOUTH AFRICAN SPECIES OF *Phthiria*

♂♂

1 (*a*) Proboscis without any hairs or dense hairs on labral part; apical part of head beyond anterior level of eyes to antennal insertions distinctly less conically prominent, produced, or narrowed, or pointed apically, appearing less tilted upwards; buccal cavity not straightly and steeply sloping backwards; abdomen without or with comparatively much narrower yellowish hind margins to tergites and, if more broadly yellowish, proboscis without hairs above 2

(*b*) Proboscis with distinct, conspicuous, fairly dense, and longish hairs on basal half above on labral part; apical part of head beyond anterior level of eyes to antennal insertions more markedly conically prominent, produced and narrowed or more pointed apically, appearing more tilted upwards; buccal cavity distinctly more straightly and steeply sloping obliquely backwards; abdomen with relatively broad and conspicuous yellowish hind margins to both tergites and sternites ♂ *pilirostris* Hesse

2 (*a*) Antennal joint 3 more spindle-shaped, or tending to be more or less equally broadened above and below at broadest part, appearing less distinctly humped, ending apically in an upper and lower spine-like process, with either both tending to be equally developed, together forming a more symmetrical bifid process, or the lower one is distinctly stronger, more prominent; head in front of eyes less markedly tumid or inflated in appearance, the frons being narrower and upper parts of genae also relatively narrower, less bulging or inflated; wings, even if appearing slightly hyaline, tinted cinereous or even dusky, without, or with only a very feeble, subopaquely milky whitish tint; hairs on head and body on the whole less dense, usually shorter and often sparse, those on legs also shorter, less dense and often poorly developed or almost absent 3

(*b*) Antennal joint 3 tending to be more distinctly humped above, sometimes conspicuously so, ending in a distinctly stronger, longer, and sometimes curved down, upper spine-like process which is always stronger than the feebler or much reduced lower one, the two together not symmetrically bifid; head in front usually distinctly more markedly tumid or inflated, the frons relatively broader, more convex, and upper genal parts also broader, more bulging and inflated and, if not, other characters conform; wings usually clear hyaline, rarely without a very distinct, or even conspicuous, subopaquely milky whitish tint; hairs on head and body, also legs, on the whole much denser, more shaggy and often longer 10

3 (*a*) Last sternite mainly yellowish or more conspicuously yellowish; legs entirely or predominently pale yellowish, or at least tibiae and bases of tarsi mainly pale yellowish 4

(*b*) Last sternite entirely dark or black, or not distinctly yellowish; legs entirely black or dark, or more yellowish brown or brownish than pale yellowish, only knees sometimes narrowly yellowish or pallid 5

4 (*a*) Entire femora, tibiae, and bases of tarsi yellowish . . ♂ *pulla* Bezzi var. *xerophila* Hesse

(*b*) Only apices or apical parts of femora, entire middle and hind tibiae, upper surfaces of front tibiae, and bases of tarsi yellowish .. ♂ *pulla* Bezzi var. *fallax* Hesse

5 (*a*) Body relatively broader and thorax distinctly less convex above, less humped; scutellum markedly transverse, distinctly very much broader than long, at least twice as broad as long; basal joint of front and hind tarsi, especially of latter, only about, or only a little more than, half length of hind tibiae; knobs of halteres darkened above in apical half .. .. ♂ *laeta* Bezzi (nec Hesse 1938: 826)

(*b*) Body distinctly narrower, the thorax distinctly more convex, more humped; scutellum distinctly less transverse, very much narrower, more conically narrowed apically, more convex and, though broader than long, usually considerably less than twice as broad as long; basal joint of front and hind tarsi, especially of the latter, much, or very much, more than half length of tibiae; knobs of halteres more extensively, or entirely, pale above and, if dark above, other characters conform 6

6 (*a*) Anterior part of head with the frons and genal parts narrower and shorter, less spout-like; antennal joint 3 usually broadened at about, or a little beyond, middle, more spindle-shaped or humped; apical joint or part of palps only slightly broadened, not spindle-shaped or spear-blade-shaped; frons and genal parts not entirely or conspicuously shining, usually duller, or in part covered with whitish or greyish tomentum, and body also distinctly less shining or predominently duller due to greyish white tomentum; hairs on frons and genae, and fine ones on abdomen above, mainly pale or whitish 7

(*b*) Anterior part of head with the frons and genal parts broader and longer, more protruding spout-like; antennal joint 3 more parallel-sided or equally broad; apical joint or part of palps distinctly more spear-blade-shaped; frons and genal parts, and even head below, more conspicuously brilliantly shining and body above, including abdomen, distinctly more shining, without greyish tomentum; hairs on frons and genae, and fine ones on abdomen above, dark or black . . ♂ *nitidigena* sp. nov.

7 (*a*) Wings clearer, more vitreous hyaline, without a very distinct subopacity and, if so, this is only very faint and scarcely perceptible, milky whitish; middle cross vein tending to be nearer middle of discoidal cell; latter relatively shorter, only a little

more than twice as long as broad; head in front and body above much duller, less shining; antennal joint 3 without distinct hairs above, usually with the apical processes more equally developed; knees narrowly, or to a variable extent, pallid or yellowish 8

(*b*) Wings less clear, with a more distinct yellowish whitish, cinereous yellowish or greyish brownish subopacity, sometimes even uniformly dusky; middle cross vein distinctly more, or even much, beyond middle of discoidal cell; latter relatively much longer, much more than twice, to nearly or even about 3 times, as long as broad; head in front, especially upper genal parts, and body above on the whole tending to be more shiny; antennal joint 3 usually with some distinct, or even conspicuous, hairs above, usually with the lower apical process distinctly more developed; knees not always yellowish and, if so, other characters do not differ . . 9

8 (*a*) Antennal joint 1 short, transverse, slightly shorter than, subequal to, or scarcely longer than joint 2; proboscis longer, usually more than 1,5 mm; knobs of halteres entirely pale or pallid above, or only darkened to a very limited extent; sides of tergites with broad bands of greyish tomentum across apical halves; last sternite tending to be reddish or yellowish to a variable extent .. .. ♂ *pulla* Bezzi
(syn. *flavigenualis* Hesse)

(*b*) Antennal joint 1 distinctly longer, elongate, nearly or quite twice length of small transverse joint 2; proboscis shorter, only about 1,5 mm long; knobs of halteres entirely dark or blackish above; sides of abdomen or tergites without distinct, or at least conspicuous, transverse apical bands of greyish tomentum; last sternite entirely dark .. .. ♂ *pulla* var. *anomalocera* n.

9 (*a*) Wings more elongate, clearer, greyish hyaline, with a slight whitish or yellowish whitish subopacity; veins paler, more yellowish; middle cross vein more beyond middle of discoidal cell which itself is relatively longer; proboscis longer, about 3–3,5 mm long; knees distinctly contrastingly yellowish; buccal rim and genae not separated by a very distinct groove .. .. .. ♂ *crocogramma* Hesse

(*b*) Wings relatively shorter, distinctly slightly infuscated, dusky or tinted yellowish brownish to even brownish throughout; veins darker, more reddish brown; middle cross vein only a little beyond middle of discoidal cell which itself is relatively shorter; proboscis shorter, relatively stouter, less than 3 mm long; knees not pallid or yellowish, but front and middle legs sometimes yellowish brownish; buccal rim and genae separated by a more distinct groove .. .. ♂ *tinctipennis* sp. nov.
(syn. ♂ *pubescens* Hesse nec Bezzi)

10 (*a*) Anterior part of head, comprising frons and genae, distinctly much more prominent, more conspicuously inflated or tumid, the frons and genae being also distinctly very much broader; antennal joint 3 markedly broadened, distinctly more humped, its upper apical spine distinctly more developed, much longer and stouter than lower process and usually more curved downwards; hairs on frons, genae and on body as a whole distinctly denser, often more woolly; whitish or greyish pruinescence on body less developed; knees, excluding the articulations, not pallid or yellowish; last sternite longer, more elongate and scoop-like 11

(*b*) Anterior part of head distinctly less prominent, less conspicuously tumid or inflated, the frons and genae being distinctly much narrower; antennal joint 3 subparallel-sided, or at least not so conspicuously broadened or humped, its upper apical spine only slightly, though distinctly, stronger than the relatively well-developed lower one; hairs on frons, genae, and body slightly less dense; whitish or greyish pruinescence on body on the whole more conspicuously developed; knees, including articulations, more distinctly pallid or yellowish; last sternite distinctly shorter
♂ *namaquensis* sp. nov.

11 (*a*) Wings distinctly and conspicuously subopaquely milky whitish; middle cross vein very much beyond middle of discoidal cell; hairs on body and legs, excepting only on head in front in some forms, entirely or predominently very pale or whitish; antennal joint 3 usually humped at middle, or only a little beyond middle .. 12

(*b*) Wings greyish hyaline, without any, or with only a feeble scarcely perceptible, whitish subopacity; middle cross vein at about, or only slightly beyond, middle of discoidal cell; hairs on head and occiput, intermixed ones on thorax, on scutellum, disc of abdomen above, coxae, and legs very dark or black, those on thorax above and to a certain extent on pleurae, and on sides in apical half of abdomen gleaming more yellowish or yellowish brownish; antennal joint 3 tending to be humped nearer apex .. .. ♂ *brunnescens* sp. nov.

12 (*a*) Antennae longer, stouter, with joint 1 distinctly much longer, at least 1½ to 2 times length of 2, with longish and dense hairs on both 1 and 2; joint 3 characteristically and prominently arched or humped at about, or just beyond, middle, with conspicuous hairs above, ending apically in a strong, finger-like, curved down, upper process, dwarfing the slight lower apical prominence; wings rather more pointed apically, the upper cubital branch ending apically at wing-point; veins dark brown to blackish brown; knobs of halteres more extensively darkened or black above; hairs on head, body, and legs distinctly and markedly much denser, longer, and more woolly or shaggy 13

(*b*) Antennae proportionally shorter, with joint 1 very much shorter, scarcely, or only a very little longer than, or subequal to, as long as, or even a little shorter than joint 2, with very much shorter, or only very short and less dense, hairs on 1 and 2; joint 3, though also humped or broadened, less strongly developed, without any, or with much feebler and shorter, hairs above, ending apically in a less stout and shorter process, less markedly curved down, forming a more bifid process with an also relatively prominent lower process; wings more rounded apically; veins paler, more yellowish or pallid and, if dark, other characters conform; knobs of halteres either entirely yellowish or pallid above, or with less extensive darkening above; hairs on head, body, and legs distinctly shorter, less dense, less woolly or shaggy .. 14

13 (*a*) Hairs on frons and genae entirely white and distinctly less dense; antennal joint 3 tending to be thicker basally; veins in wings darker; knees more distinctly, even though obscurely, yellowish .. .. ♂ *lanigera* Bezzi (typical)

(*b*) Hairs on frons, antennae above, and upper halves of genae black and distinctly denser; antennal joint 3 tending to be thinner basally; veins in wings tending to be paler, more yellowish or with more yellowish; knees not perceptibly yellowish ♂ *lanigera* var. *melampogon* n.

14 (*a*) Second marginal cell in wings not acuminate or acute at base; anterior part of head distinctly more bulging, inflated, or tumidly prominent, the frons and genae being longer (or broader), length of genae at broadest part on sides of head quite, or nearly, half length of eye at same level; antennae relatively longer, joint 3 distinctly and relatively longer, more spindle-shaped, its upper apical process longer and stouter relative to lower one to a variable degree; palps proportionally longer, more projecting; hairs on head in front and on body distinctly denser and longer; scutellum on the whole more acute or pointed apically; basal joint of hind tarsi about, or only a little more than, half length of hind tibiae 15

(*b*) Second submarginal cell distinctly more acute or acuminate at base; anterior part of head distinctly less prominently inflated or tumid, the frons and genae being shorter (narrower), the length of genae at broadest part on sides of head very much less than half, only about, or nearly a little more than, a third length of eye at same level; antennae relatively and proportionally shorter, joint 3 distinctly more oval or slightly elongate-oval, its upper apical process scarcely, or only a very little, longer than lower one, the two together forming a more bifid process; palps proportionally much shorter, less projecting; hairs on head, body, and legs distinctly shorter, less dense; scutellum more rounded apically; basal joint of hind tarsi distinctly much more than half length of hind tibiae .. .. .. ♂ *ovalicornis* sp. nov.

15 (*a*) Frons and genae with dark blackish brown or black hairs; palps and legs slightly paler, more pale yellowish brown to sienna brownish; proboscis longer, about 2–2,5 mm; veins in wings pallid or yellowish and those between anal and axillary cells and anal and fourth posterior cells markedly straight; apical stalk of anal cell on the whole longer, subequal to, or as long as, apical cross vein of discoidal cell; antennal joint 3 shorter, broader, more spindle-shaped, its upper apical process on the whole stouter, blunter, scarcely or not much curved and the lower apical part more prominent .. .. ♂ *nigribarba* Hesse

(*b*) Frons with dark, or some dark, hairs, but genae entirely white-haired; palps and legs much darker, darker brownish or black; proboscis shorter, only about 1,5 mm long; veins in wings darker and those between anal and axillary and anal and fourth posterior cells not entirely or so markedly straight; stalk of anal cell shorter than apical cross vein of discoidal cell; antennal joint 3 more elongate, slightly more than twice as long as joints 1 and 2 combined, not so obviously spindle-shaped, its upper apical process slightly longer, more slender, more acute apically, and more curved downwards to the scarcely prominent lower apical angle ♂ *simmondsii* Hesse

♀♀

1 (*a*) Proboscis without any hairs or dense hairs on labral part; apical part of head beyond anterior level of eyes to antennal insertions less conically produced, prominent, narrowed, or pointed apically, appearing less tilted upwards, the buccal cavity not straightly and steeply sloping backwards and, if rarely so, proboscis without hairs above; body not predominently, or almost entirely, yellowish above and below and, if greater part of body is not black, the thorax above and basal halves of tergites at least black or more extensively black 2

(*b*) Proboscis with distinct, conspicuous, fairly dense and longish, yellowish or golden-gleaming hairs on at least basal half of labral part above; apical part of head, beyond eyes to antennal insertions, distinctly more markedly conically prominent, produced, narrowed, and more pointed apically, appearing more tilted upwards, the buccal cavity distinctly more straightly, steeply sloping obliquely backwards; body predominantly, almost entirely yellow or yellowish above and below, even thorax above with only three reddish brown or brownish fasciae, and only extreme bases of tergites discally above and an infusion on hypopleural part dark ♀ *pilirostris* Hesse

2 (*a*) Antennal joint 3 more spindle-shaped, usually more equally broadened above and below at broadest part, appearing less distinctly humped, ending apically in an upper and lower spine-like process either more or less equally prominent and together forming a more or less bifid process, or with a tendency for lower one to be stronger; head in front less tumidly prominent, the frons distinctly less broadly transversely convex and upper parts of genae not so continuously tumid or convex with frontal convexity; wings, even if with some degree of subopacity, not distinctly tinted subopaquely milky whitish; vestiture on body and legs distinctly less dense, much sparser, or shorter, often almost wanting; body usually with extensive yellow, rarely mainly black 3

(*b*) Antennal joint 3 tending to be more distinctly humped above, sometimes conspicuously so, ending in a distinctly longer or stronger, sometimes curved down, upper process and a more reduced, sometimes scarcely detectable, lower prominence, rarely with both more or less equally developed and, if so, other characters listed here do not differ; head in front slightly or distinctly more tumidly prominent or protuberant, the frons distinctly more convex, more transversely so, relatively broader, and upper parts of genae also relatively more convex or tumid and continuously so with frons and, if not apparent, other characters conform; wings rarely not distinctly, often conspicuously, tinted subopaquely milky whitish; vestiture on body and legs usually distinctly more conspicuous, denser, and usually longer; body mainly black or dark, without any, or with very little, yellow present .. 13

3 (*a*) Body with distinctly much or more yellow, the head, at least sides of thorax above, scutellum, hind margins of tergites, pleurae, venter, and sometimes legs conspicuously yellow or orange yellow to a variable, greater or lesser, extent; genae, head below, scutellum, and rest of body above not, or distinctly less, shiny, not tending to be brilliant; wings usually more hyaline and, if distinctly tinted greyish or dusky, body with much yellow 4

(*b*) Body entirely black, without any yellow markings, the legs entirely very dark blackish brown or black, and even knees not markedly paler; genae, head below, scutellum, and to a certain extent integument of rest of body above distinctly more brilliantly shining and smooth; wings distinctly, though faintly, tinged slightly subopaquely greyish yellowish or cinereous yellowish, even with a faint brownish tint in certain lights .. .. ♀ *pubescens* Bezzi

4 (*a*) Legs, including coxae, entirely or predominantly pale yellowish or at least mainly, or more extensively yellowish; almost entire prosternal part, pleural parts below wings, and hind margins of sternites usually entirely, predominantly, or at least more extensively yellowish and, if not, legs are yellowish; upper apical process of antennal joint 3 either nearer apex or almost as long as or as strongly developed as lower one, the two together forming a more symmetrical bifid process and, if not, legs at least mainly yellowish 5

(*b*) Legs, including coxae, entirely very dark, blackish brown, or black, or with much black, only the knees sometimes pallid or yellowish; prosternal part, pleural parts below wings mainly dark or black, and hind margins of sternites, if not black, usually more obscurely, or only narrowly, yellowish; upper apical process of antennal joint 3 either farther back from apex or smaller, shorter, and less developed than lower one, the two together usually forming a more asymmetrical bifid process .. 10

5 (*a*) Body relatively broader and thorax distinctly less humped; head and frons relatively much broader; scutellum markedly or more obviously transverse, distinctly very much broader than long, quite, or more often, a little more than twice as broad as long; basal joint of hind tarsi only about, or only a little more than, half length of hind tibiae; front femora above and outer hind faces of tibiae more distinctly darkened 6

(*b*) Body relatively narrower, the thorax distinctly more convex above, more humped; head and frons narrower; scutellum less transverse, relatively or distinctly much narrower, more conically narrowed posteriorly and, though broader than long, usually considerably less than twice as broad as long; basal joint of hind tarsi distinctly very much more than half length of hind tibiae; front femora and outer faces of tibiae not, or scarcely, darker and, if much darkened, other characters do not differ 8

6 (*a*) Broadish hind border, or almost hinder half, and sometimes narrow base of scutellum, black; yellow hind margins of tergites distinctly broader, occupying almost, or about, the apical halves of tergites on sides; yellow on sides of thorax above relatively narrower; lateral extension of black frontal fascia on frons anteriorly more constant and broader, usually reaching eye; hairs on tergites distinctly less dense, relatively shorter, and those discally more whitish; fine hairs on frons also less dense, more whitish; tarsi tending to be paler, or more yellowish, basally or in basal part ♀ *laeta* Bezzi

(*b*) Entire scutellum discally yellow; yellow hind margins of tergites distinctly narrower, occupying less than apical halves of tergites on sides; yellow on sides of thorax above usually broader; black medial frontal fascia either not extending laterally on frons in front, or the extension is narrower or spot-like; hairs on tergites distinctly denser, relatively longer, and distinctly sericeous yellowish to pale golden discally; fine hairs on frons denser, more golden; tarsi tending to be entirely dark or black .. 7

7 (*a*) Antennal joint 3 ending apically in two almost equally strong upper and lower processes, the upper one scarcely much smaller than lower one and tending to be nearer apex, the two together forming a distinctly more symmetrical bifid process; upper surface of front femora and sometimes a subapical infusion on inner or upper apical part of the others and outer faces of all the tibiae more conspicuously or intensely darkened; knobs of halteres with a dark spot or darkened on outer margin or sides above .. .. ♀ *flaviscuta* sp. nov. (and forms of it)

(*b*) Antennal joint 3 ending apically in two unequally developed processes of which the upper one is much weaker and thinner than the much stouter lower one and also farther from the apex, the two together forming a distinctly more asymmetrical bifid process; upper surface of front femora and outer surfaces of all the tibiae not, or only feebly and less conspicuously, darkened; knobs of halteres not distinctly darkened in part or with a spot above .. .. ♀ *hesperia* sp. nov.

8 (*a*) Wings vitreous hyaline, without any, or scarcely any, detectable subopacity; black on head more reduced, that on occiput less extensive, that on head above more or less narrowly confined to ocellar tubercle, or as a narrow line towards middle, and as a spot anteriorly on each side of antennae, without a broadish central band on head below, and buccal rims and buccal cavity also pale; yellow on pleural parts

distinctly much more extensive, greater part of pleurae above coxae being entirely or predominantly yellow; yellow on sides of thorax broader, more extensive, and with a tendency for two yellowish submedial lines above as well, and base of thorax above yellowish or orange yellowish to a variable extent; scutellum entirely yellowish; transverse black basal bands across tergites almost confined to middle above; antennae with joint 1 more transverse, about as long as, or subequal to, joint 2, usually yellowish or at least yellowish above, with joint 3 more spindle-shaped or humped, without any distinct hairs above 9

(*b*) Wings distinctly dusky, tinted subopaquely cinereous yellowish to brownish; black on head distinctly more developed, almost the entire occiput and a broad central fascia from it across ocellar tubercle to antennae black, without a spot on each side of antennae, but with the buccal rims and buccal cavity dark, and a central broad fascia on head below also black; yellow on pleural parts distinctly more reduced, present only as a propleural spot, a central band across upper part of sternopleuron, spots behind pteropleuron and on metapleural part; yellow on sides of thorax much narrower, the entire discal part black, and base of thorax above black; scutellum yellowish only on disc, its broad declivous sides black; transverse black basal bands across tergites extending down sides as well; antennae with joint 1 entirely black, slightly more elongate, tending to be slightly longer than 2, with joint 3 scarcely or not broader across middle, not distinctly humped, and with distinct and conspicuous hairs above .. .. ♀ *tinctipennis* sp. nov.

9 (*a*) Hairs on body, and especially on abdomen, distinctly much sparser, less conspicuous, shorter, and sometimes almost absent.. ♀ *pulla* Bezzi var. *xerophila* Hesse

(*b*) Hairs on body, and especially on abdomen, distinctly much denser, longer, more conspicuous .. .. ♀ *pulla* Bezzi var. *fallax* Hesse

10 (*a*) Yellow or orange yellow transverse bands across hind margins of tergites distinctly very much broader, occupying nearly, or even about, apical half of tergites; yellow on sides of thorax relatively broader, the fascia across sternopleuron occupying almost entire upper part of it, and scutellum with less black on declivous sides; wings relatively broader and longer, without, or with scarcely detectable or feebler, subopacity; proboscis longer, not shorter than 2 mm 11

(*b*) Yellow transverse bands across hind margins of tergites and sternites distinctly very much narrower, those of tergites occupying considerably less than apical halves; yellow on sides of thorax relatively narrower, the fascia across sternopleuron occupying only hinder upper half, and scutellum with more extensive black on declivous sides; wings relatively shorter and narrower, with a more conspicuous subopaquely milky whitish tint; proboscis shorter, only about 1,8–2 mm

♀ *cognata* Hesse

11 (*a*) Proboscis distinctly stouter, longer, about 2,8–3,5 mm; occiput with some yellow behind eye-margins, either on vertex or right around eyes; anterior spiracle with more yellow around it; yellow hind margins of tergites broader, not much less than apical half of tergites; legs on the whole darker, with broader yellowish knees; wings with a distinct, though feeble, subopacity 12

(*b*) Proboscis more slender, shorter, only about 2 mm long; entire occiput behind eyes in at least upper half black; anterior spiracle without any, or with scarcely any, yellow; yellow hind margins of tergites narrower; legs with more yellowish brown or yellowish on femora, especially on inner upper surfaces on at least basal halves, and front coxae pale in front, and knees not, or less broadly, yellowish; wings more vitreous hyaline, without any detectable subopacity .. ♀ *varipes* sp. nov.

12 (*a*) Thorax entirely black above; yellow on sides of thorax in front slightly narrower, and scutellum with more black on declivous sides; yellow hind margins of tergites narrower, occuyping only about apical halves of tergites; frons with a consistent broad central black band extending to antennae; wings clearer hyaline

typical ♀ *crocogramma* Hesse

(*b*) Base of thorax yellowish or yellowish-spotted to a variable extent; yellow on sides of thorax relatively broader, and scutellum without, or with much less, dark on declivous sides; yellow hind margins of tergites broader, occupying more than apical halves of tergites; black fascia on frons much reduced, either wanting or thinning out anteriorly; wings with a slight, but distinctly more evident, subopacity .. .. ♀ var. of *crocogramma* Hesse

13 (*a*) Antennae with joint 1 distinctly much longer, at least 1½ times to nearly, or about, twice length of 2, with joint 3 usually distinctly more humped, ending in a conspicuous, slightly curved, upper process which dwarfs the scarcely detectable lower one; head in front distinctly more conically prominent or produced; head below, propleural callosity above front coxae, and a longitudinal fascia along middle of pleurae, ivory yellowish or yellow; hairs on head, body, and legs distinctly longer, markedly denser, and more woolly or shaggy 14

(*b*) Antennae with joint 1 much shorter, subequal to, as long as, or scarcely longer than, 2, with joint 3 usually not so conspicuously humped, sometimes more spindle-shaped, or subparallel-sided, or even oval, ending apically in a relatively less developed upper process which usually forms a more evident bifid process with the lower one which itself is only a little shorter; head in front distinctly less prominent, not conically produced; head below, or at least greater part of it below, and pleurae, either entirely black or not with yellowish on all the above-mentioned sites; hairs on head, body, and legs distinctly shorter, relatively less dense, less woolly or shaggy 16

14 (*a*) Head in front broader, less conically prominent; antennal joint 3 more conspicuously humped, with conspicuous hairs above, ending apically in a longer, stouter, finger-like process; frons entirely black; head below without a central dark fascia; scutellum more broadly rounded; hairs and scaling on body and legs distinctly much denser and longer, those above brassy or golden yellow; slightly larger and more bulky forms, usually more than 4,5 mm long 15

(*b*) Head (cf. Fig. 1D) in front narrower, distinctly more conically prominent or produced; antennal joint 3 less conspicuously humped, without any conspicuous hairs above, ending in a shorter, less stout, upper process; frons with a yellow stripe on each side along eye-margins; head below with a central dark fascia; scutelum distinctly more conically pointed or narrowed apically; hairs and scaling on body and legs less dense, shorter, and those above distinctly silvery white; slightly less bulky forms, only about 4,4 mm long, with a wing-length of about 4,2 mm ♀ *conocephala* sp. nov.

15 (*a*) Upper part of genae smooth, without hairs, or with a few pale ones; wings distinctly less conspicuously milky whitish, with darker, darker brownish, or blackish brown veins; knobs of halteres usually with a variable dark spot above; knees more distinctly yellowish .. .. ♀ *lanigera* Bezzi

(*b*) Upper part of genae with a dense tuft of black hairs; wings distinctly and more conspicuously milky whitish, the veins distinctly paler, more yellowish brown or yellowish; knobs of halteres entirely ivory whitish or yellowish above; knees not, or scarcely perceptibly, yellowish .. .. .. ♀ *lanigera* var. *melampogon* n.

16 (*a*) Genae and head below entirely black; pleural parts entirely black; antennal joint 3 more spindle-shaped or oval; wings with the veins very pale, pallid or yellowish, the middle cross vein usually much beyond middle of discoidal cell; apical stalk of anal cell longer, at least as long as, or even longer than, apical cross vein of discoidal cell; knobs of halteres entirely very pale or pallid above; basal joint of hind tarsi usually about, or scarcely more than, half length of hind tibiae 17

(*b*) More than lower half of genae and continuous as a narrow streak round margin of eyes to about halfway up behind eyes pallid; small, middle, boss-like prominence in middle of pleurae between sterno- and hypopleurae and pteropleuron, and sometimes even to a certain extent on adjacent parts of sterno- and metapleuron, also pallid; antennal joint 3 tending to be more subparallel-sided, less broadened at middle; wings with the veins distinctly darker, more brownish to blackish brown, the middle cross vein only a little beyond middle of discoidal cell; apical stalk of anal cell shorter, markedly short, much shorter than apical cross vein of discoidal cell; knobs of halteres slightly darkened above or with a variable dark infusion; basal joint of hind tarsi distinctly much more than half length of hind tibiae ♀ *namaquensis* sp. nov.

17 (*a*) Base of second submarginal cell more normal or at least not markedly acute; antennal joint 3 relatively longer, more spindle-shaped, its upper apical process distinctly stouter and longer than lower one, the apex less bifid in appearance; greater part of palps luteous or yellowish; legs on the whole paler, with more yellowish or yellowish brown, the apical parts of femora and the tibiae, and greater part of tarsi pale yellowish or luteous; hairs relatively less dense, but slightly longer ♀ *nigribarba* Hesse

(*b*) Base of second submarginal cell distinctly much more markedly acute; antennal joint 3 (cf. Fig. 1E) relatively shorter, more oval, its upper apical process not much, or scarcely, longer than lower one, the apex thus more symmetrically bifid; palps dark; legs, including tibiae, distinctly much darker, mainly blackish brown or black, only the knee-articulations being reddish brownish, and bases of tarsi tending to be dark sienna or reddish brownish; hairs relatively shorter, but distinctly much denser .. .. ♀ *ovalicornis* sp. nov.

Subfamily **Usiinae** Becker

This subfamily, originally based on the typical Palaearctic genus *Usia* Latreille, was supposed by me (Hesse 1938: 712) not to be represented in southern Africa after the transference of the genera *Corsomyza* Wied. and *Hyperusia* Bezzi, which Bezzi (1924: 103–109) placed in the Usiinae, to the Bombyliinae (Hesse 1938: 712–713).

Recently Hull (1973:212-211) however emended and redefined this subfamily, restricting it to four genera of which two, *Usia* Latreille and *Dagestania* Paramonov, are Palaearctic and Oriental in their distribution and two, *Apolysis* Loew and *Oligodranes* Loew, occur not only in the Palaearctic and Nearctic Regions but also in the Ethiopian Region including the South African subregion.

As a result of Hull's taxonomic assignment of genera in this subfamily the latter two genera which I placed in the subfamily Phthiriinae in my revision (Hesse 1938: 822) are now to be considered as important South African representatives of the emended subfamily Usiinae.

Genus *Apolysis* Loew

Apolysis: Hesse, 1938: 848. Hull, 1973: 217.

The discovery of still other South African species of this genus does not appear to necessitate much change in the diagnostic characters recorded by Loew (1860) and Engel (1933: 127) and supplemented by me in 1938, and more fully detailed by Hull in 1973. Worthy of record however are that in the case of the South African forms the wings appear to be more frequently distinctly tinted milky whitish, that the abdomen of both sexes in some species is often entirely or predominantly pallid or yellowish, that the legs of certain species are relatively short and stoutish, and that the hind femora of still others are slightly curved.

Descriptions of new species and comments on already described ones are as follows:

Apolysis monticola sp. nov.

Fig. 2D

In the absence of the ♂, these ♀♀ are here described as a new species even though they appear to be very near the ♂ *xanthogaster* Hesse (1938: 853, fig. 259). They are characterized as follows:

Body and legs mainly black; integument dull, with very faint greyish white bloom on head, thorax above, and scutellum; hind margins of tergites narrowly pallid or yellowish, those of sternites more broadly yellowish, sometimes very much so or even with greater part of venter, apart from the broad pallid hind margins, reddish yellow, and with at least the sides (articulating part between tergites and sternites) conspicuously yellowish; legs sometimes, or at least the tibiae, more castaneous brown.

Vestiture with the hairs, even on head and thorax, very sparse, entirely pale or whitish, those on abdomen short and a little longer posteriorly; those on legs short, not conspicuous.

Head with antennal joint 1 distinctly longer than 2, about 1½–2 times as long; joint 3 distinctly slightly produced and rounded apically beyond the spine which is dorsal and subapical in position; proboscis stoutish, about 0,6–1 mm long; palps longish, distinctly projecting, at least as long as antennal joints 2 and 3 combined, and usually about as long as antennae.

Wings (cf. Fig. 2D) greyish hyaline, with a very faint greyish white sub-opacity in certain lights; veins brown to dark brown; first basal cell a little longer than second, and part of third vein between it and apical cell sub-equal to, as long as, or even slightly longer than, cell itself; knobs of halteres entirely whitish.

From 6 ♀♀, including the holotype, in the South African Museum.

Length of body: about 2,2–3,12 mm
Length of wing: about 2,3–3,4 mm

Distribution

Natal: Cathedral Peak in Natal Drakensberg, alt. 1 950 m (B. Stuckenberg, March 1955).

The darker legs, the relatively longer wings, slightly longer first basal cell, relatively longer second submarginal cell, much darker veins, and shorter proboscis distinguish this species from the ♂ *xanthogaster* which also comes from the Drakensberg on the Orange Free State side.

Apolysis thamnophila sp. nov.

A species very near the preceding species and also *cingulata* Hesse (1938: 853).

From *monticola* it differs in having the integument of body above distinctly more shining, distinctly broader yellowish hind margins to the tergites, dark hairs on thorax above posteriorly and on scutellum, shorter and sparser hairs on abdomen, a first basal cell which is as long as second, and very much shorter than distance between first basal cell and base of second submarginal cell.

From ♀ *cingulata* Hesse it differs in being relatively smaller, 2,2 mm as against 3,5 mm and with a wing-length of only about 2,4 mm as against 4 mm, in having a darker buccal rim, narrower ivory yellowish hind margins to tergites, entirely dark legs, including knees, more whitish hairs on occiput, darker hairs on thorax posteriorly and on scutellum, entirely yellowish white halteral knobs, shorter proboscis, only about 1 mm long as against 2 mm in *cingulata*.

From a single ♀ specimen in the South African Museum.

Distribution

Little Karoo: Rust en Vrede near Oudtshoorn (Museum expedition, October 1951).

Apolysis stuckenbergi sp. nov.

Fig. 2A

This species which belongs to the *humilis* section is named after Dr B. Stuckenberg of the Natal Museum who is a great South African dipterist and who has collected many interesting species of *Bombyliidae* in Natal. The species is characterized as follows:

Body black; hind margins of tergites and sternites narrowly and obscurely pallid or whitish in ♀; legs entirely very dark blackish brown to black; integument of body dull, with dull greyish white bloom, absent on thorax above in ♂, but in ♀ separated by two submedial dark lines and a broken lateral one.

Vestiture with the hairs on body and legs sparse, longer in ♂ than in ♀, entirely whitish.

Head with the eyes in ♂ in contact in front of ocellar tubercle, separated in ♀, on vertex nearly, or quite, 3 times width of tubercle; transverse frontal depression in ♀ at about middle and the middle longitudinal depression from the ocellar tubercle ending in it; antennal joint 1 distinctly longer than 2, at least 1½ times as long as 2; joint 3 (cf. Fig. 2A) elongate, with a rather distinct prominence in front of apical spine, the latter dorsal and subapical in position, with the apex of joint beyond spine slightly produced and rounded; proboscis (cf. Fig. 2A) about 1–1,2 mm long, slightly stouter in ♀; palps long, projecting conspicuously, nearly or quite as long as antennae.

Wings greyish hyaline; veins dark blackish brown; first basal cell a little, but distinctly, longer than second, shorter than distance between it and second submarginal cell; second posterior cell widely divergent apically; knobs of halteres darkened or black above in ♂, usually entirely whitish in ♀ or sometimes with a small darkish spot above.

Legs slender; first basal joint of hind tarsi a little less than half length of hind tibiae.

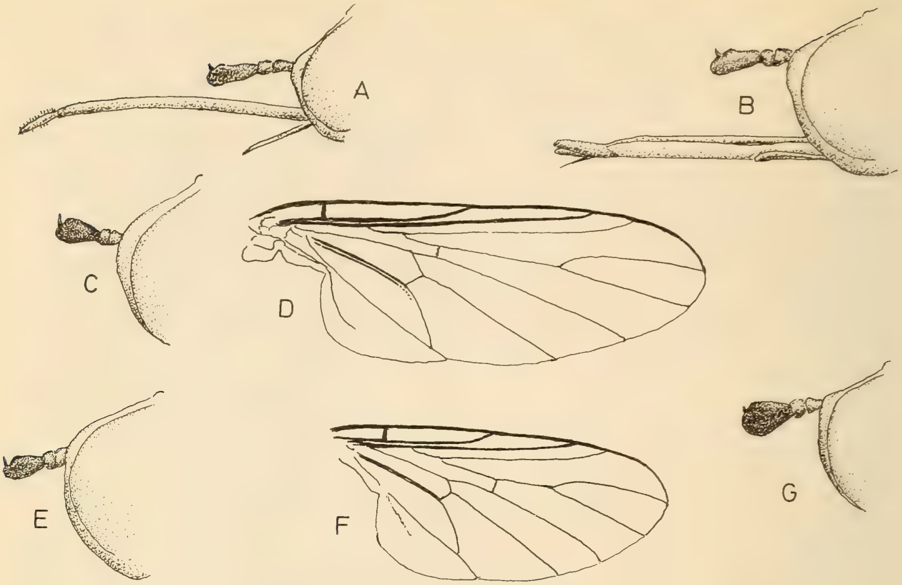

Fig. 2. Left side views of heads and antennae, and right wings of some new species of *Apolysis*. (All to the same scale.)
A. ♀ *stuckenbergi;* B. ♀ *capicola;* C. ♀ *brachycera;* D. ♀ *monticola;* E. ♀ *seminitens;* F. ♀ *semiflava;* G. ♂ *hirtella.*

From 5 ♂♂ and 5 ♀♀ (♂ holotype in the Natal Museum, ♀ allotype in the South African Museum).

Length of body: about 1,8–2,2 mm
Length of wing: about 2,12–2,6 mm

Distribution

Natal: Karkloof (B. Stuckenberg, 1 April 1956).

From *humilis* Loew it differs mainly in being smaller, with entirely whitish hair on occiput, thorax above, and scutellum, and slightly less cinereous-tinted wings.

Apolysis oreophila sp. nov.

Some other ♀♀ from the Drakensberg in Natal resemble ♀♀ of the preceding species *stuckenbergi* so closely that they may almost be considered as only representing a variety of the latter. In the absence of the ♂ and the slight differences present in these ♀♀ they are here considered as a distinct species.

They differ from *stuckenbergi* in being distinctly larger, about 2,4–3 mm, with a greater wing-length of about 3–3,2 mm (as against 2,12–2,6 mm in the latter); in having the subopacity of the wings in certain lights more distinctly, though faintly, whitish and not cinereous, and with the veins more yellowish brown than blackish brown; apical stalk of anal cell apparently shorter, subequal to, or even shorter (not a little longer) than apical cross vein of second basal cell; hairs on body and legs distinctly longer, relatively more dense, and the fine hairs on hind tibiae longer, more conspicuous; and in having slightly broader and more constantly pallid hind margins to the abdominal segments, especially the sternites.

From 6 ♀♀ (holotype in the Natal Museum and paratypes in the Natal and South African Museums).

Distribution

Natal: Cathedral Peak area in the Natal Drakensberg, alt. 1 950 m (B. Stuckenberg, 23 March 1955).

Apolysis capicola sp. nov.

Fig. 2B

This southern Cape species is referable to the *xanthogaster* and *monticola* section, but may also be compared with the *stuckenbergi* and *oreophila* section. It agrees and differs from these species mentioned in the following respects:

Body, including legs, mainly black; integument entirely dull, thus differing from *cingulata* and *thamnophila*; hind margins of tergites scarcely, or only very narrowly, pallid in ♂, those of sternites in ♂ narrowly pallid, the tergites in ♀ sometimes as in ♂, but sometimes, especially those posteriorly, narrowly and distinctly pallid or yellowish, broader so than in ♂, and hind margins of sternites in some ♀♀ relatively broadly yellowish, more like those of some ♀♀ of *monticola* and thus distinctly broader so than in *stuckenbergi* and *oreophila*,

Vestiture on body distinctly not very dense, entirely sericeous whitish. even on thorax above.

Head with the eyes in ♂ in contact above for about 2,4–2,8 times length of ocellar tubercle; interocular space on vertex in ♀, at narrowest part, distinctly slightly broader than length of antennal joint 3 (sub-equal to length of joint 3 in ♀ *monticola*); antennae (cf. Fig. 2B) with joint 1 short, subequal in length to 2 or scarcely longer than 2 (distinctly or much longer than 2 in *monticola*, *stuckenbergi* and *oreophila*); joint 3 with the dorsal prominence in front of subapical excavation not, or distinctly less angularly, prominent than in *stuckenbergi* and *oreophila*; palps relatively stoutish, subequal in length to, or scarcely longer than, antennae (more slender and longer in *monticola* and the latter two species); proboscis (cf. Fig. 2B) stouter and appearing shorter than in *stuckenbergi* and *oreophila*.

Wings differing from those of all the species mentioned in being distinctly, though faintly, tinted subopaquely milky whitish; veins yellowish brown to brown; first basal cell scarcely longer than second; second posterior cell slightly divergent apically; knobs of halteres darkened or black above in ♂, entirely whitish in ♀, but in some ♀♀ also slightly darkened above.

Legs with the basal joint of hind tarsi only a very little less than half length of hind tibia.

From 6 ♂♂ and 25 ♀♀, including the ♂ holotype and ♀ allotype, in the South African Museum.

Length of body: about 1,84–2,84 mm
Length of wing: about 1,8–3,04 mm

Distribution

South-western Cape: Pearly Beach in Bredasdorp District (South African Museum expedition, December 1958) (holo- and allotypes); Wit River Valley, Bainskloof near Wellington (November 1937); Leipoldtville (South African Museum expedition, November 1956).

Apolysis fumalis Hesse

Apolysis fumalis Hesse, 1938: 855.

Since my description of the ♀ of this species in 1938 the ♂ has also been taken and the following supplementary notes on the species have to be added:

Body of ♂ entirely black; integument of thorax above in ♂ without the brownish grey bloom of ♀; legs dark chestnut brown.

Vestiture with the hairs on occiput in both sexes, those on genae and head below in ♂, and those on rest of body in ♂, including those on coxae and greater part of legs dark blackish brown to black, those on thorax above, scutellum and abdomen above in ♀ sometimes also more brownish or brownish yellow than yellow.

Head in ♂ with the eyes, in front of ocellar tubercle, in contact for a distance nearly 3 times length of the tubercle; antennal joint 1 in both sexes quite twice as long as joint 2; proboscis about 1,4–1,8 (or 2) mm long; palps long, conspicuous, and in ♂ and some ♀♀, as long as antennae.

Wings distinctly dusky or smoky brownish, darker in ♂ than in ♀; first basal cell longer than second, longer than part of third vein between it and second submarginal cell; second posterior cell widely divergent apically; knobs of halteres in ♂ entirely dark castaneous brownish.

Legs with the basal joint of hind tarsi much more than half length of hind tibia.

The original ♀ holotype is in the British Museum (Natural History), the ♂ allotype is in the South African Museum.

Length of body: about 3–3,5 mm
Length of wing: about 3,8–4,5 mm

Distribution

Natal: Karkloof (B. Stuckenberg, 1 April 1956) (♂ allotype and the other ♀♀).

Apolysis minuscula sp. nov.

A minute aberrant species which is characterized as follows:

Body mainly black, the integument smooth, polished and shining; hind margins of tergites (broadened on extreme sides), the slightly broader hind margins of sternites, and the broad articulating part on each side below between tergites and sternites in ♀ ivory yellow or yellow: hind margins of tergites in ♂ only very narrowly or obscurely yellowish, evident only on sides posteriorly; antennae, proboscis and legs yellowish brown to dark castaneous brownish, though antennal joints 1 and 2 sometimes paler.

Vestiture with the hairs on body and legs, and even head, fine, very short and sparse, inconspicuous, almost imperceptible or wanting, even in ♂, and, where detectable, apparently dark.

Head with the eyes in ♂ broadly separated above, a little more than half width of the interocular space in ♀; frons medially foveately depressed in basal half in front of anterior ocellus, somewhat tumidly convex and rounded anteriorly, more evident in ♀, the head thus more rounded anteriorly above; antennal joint 1 a little longer than 2; joint 3 more elongate ovate in ♂, usually more ovate in ♀, at least half as broad as long; proboscis, relative to body, markedly long, about 0,68–1,5 mm; palps shorter than antennae, not very conspicuously visible and not projecting much.

Wings vitreous hyaline, with a scarcely detectable milky whitish tint or subopacity in certain lights; veins or parts of veins in anterior half of wings yellowish, their distal parts, or veins in posterior half, paler, more whitish; first basal cell as long as second, much shorter than part of third vein between it and second submarginal cell; second posterior cell widely divergent apically; apical stalk of anal cell markedly long, relatively longer than in in other known South African species of this genus, at least twice as long as base of third posterior cell.

Legs with the basal joint of hind tarsi much shorter than half length of hind tibia, sometimes even only a third of its length.

1 ♂ and 6 ♀♀, including the ♀ holotype and ♂ allotype, in the South African Museum.

Length of body: about 1,2–1,7 mm
Length of wing: about 1,6–1,9 mm

Distribution

Bushmanland: Between Springbok and Pella (Museum staff, October 1939) (♀ holotype and 3 ♀ paratypes); Aggenys (Museum staff, October 1939) (♂ allotype and a ♀ paratype). North-western Cape: Kenhardt area (Museum staff, October 1939) (1 ♀ paratype).

Frequents flowers of *Mahernia grandiflora* and *M.nana*, and is easily recognized by its small size, cyrtosiine appearance, smooth and shining integument, and almost entire absence of vestiture.

Apolysis lindneri Hesse

Apolysis lindneri Hesse, 1962: 1, fig.

This is a very small species which Dr E. Lindner of the 'Staatliches Museum für Naturkunde in Stuttgart' caught on the yellow flowers of the composite *Chrysanthemoides monilifera* when he visited Cape Town in 1958 and which I described in 1962.

It differs from all the other known South African species of *Apolysis* except the preceding *minuscula*, in its small size. It is characterized as follows:

Body, including antennae and proboscis, entirely dark, dark blackish brown; eyes reddish brown; hind margins of sternites slightly narrowly pallid or pale.

Vestiture in form of fine, not very dense, greyish bloom on head, thorax, abdomen, and pleurae, and shortish, somewhat sparse hairs, slightly longer on sides of thorax anteriorly, on scutellum posteriorly, and on abdomen; these hairs gleaming pale on sides of head behind eyes, darker on occiput, pale on sides of thorax and on scutellum, darker on disc of thorax, more pale on abdomen, pale, shortish and sparse on legs, slightly longer and denser along outer hinder surfaces of hind tibiae.

Wings rather narrowish, slightly longer than body, greyish hyaline, but distinctly faintly milky whitish in certain lights; veins brownish, even fine hind margin and microtrichial fringe dark; first basal cell very slightly longer than second, distinctly shorter than part of vein between it and apical cell; latter cell slightly shorter than this same part; second posterior cell divergent apically; apical stalk of anal cell rather long, nearly twice length of base of third posterior cell; knobs of halteres whitish.

Head with the frons parallel-sided, slightly broader than width of eye (front view), slightly transversely depressed across middle, the apical part only slightly convex; antennal joint 1 subequal to 2, the two together slightly shorter than joint 3; the latter about 2,5 times as long as broad; proboscis rather stoutish, only about 0,68 mm long; palps short, not perceptibly projecting.

Legs rather slender and long, the tarsi elongate, with the basal segment of hind ones quite, or nearly, half length of hind tibiae.

From the single ♀ specimen in the Museum in Stuttgart.

Length of body: about 1,2 mm (excluding proboscis)
Length of wing: about 1,6 mm

Distribution

Western Cape Province: Cape Town (E. Lindner, 31 October 1958).

From *minuscula*, the other minute species from north-western Cape, it may at once be distinguished by the duller head and body, covered with fine greyish bloom, the longer and denser hairs on thorax and abdomen and legs, absence of distinct and conspicuous yellowish hind margins to tergites and sternites, a first basal cell in wings which is slightly longer than the second, slightly longer, more slender legs, with relatively longer basal joint tarsi, longer basal joint of hind tarsi, and slightly shorter and stouter proboscis.

Apolysis thornei Hesse

Apolysis thornei Hesse, 1938: 857, fig. 261.

Of this species the South African Museum has since obtained a very long series of both sexes from flowers of *Mahernia brandiflora* and *M. nana* in Bushmanland, north-western Cape and the Koup Karoo.

From this series it is quite evident that the species is variable and that certain statements made by me in 1938 have to be modified somewhat.

In the first place specimens (more typical form) from Bushmanland, north-western Cape, and Nieuveld Karoo have the hind margins of the tergites in the ♀♀ only narrowly yellowish, more broadly yellowish only at apex of abdomen; the wings slightly more apparently milky whitish; costal cell relatively broad at middle; and knobs of halteres in ♂♂ darkened above.

Specimens from the Koup Karoo have the hind margins of the tergites distinctly or very much broader yellowish.

Some ♀♀ from Bushmanland are entirely black, without any yellowish or pallid hind margins, and with the integument of the entire body above shining, and with the wings distinctly less milky whitish, more vitreous hyaline.

Some ♂♂ from Namaqualand have not only the wings less milky whitish, but the knobs of halteres entirely pallid.

Some ♂♂ from the Moordenaars Karoo near Laingsburg have not only pallid halteral knobs, but much yellowish on abdomen and even more yellowish legs.

Apolysis semiflava sp. nov.

Fig. 2F

This species which belongs to the *thornei* section and which, like *thornei* and some other species, frequents the flowers of a species of *Mahernia*, is easily recognized by the following characters:

Body with the head, thorax (except slightly yellowish humeral angle and postalar margin in ♀), and scutellum black; abdomen in ♀ entirely very pale yellowish, the hind margins of segments sometimes even more whitish; abdomen in ♂ with the hind margins of tergites narrowly pallid or yellowish to a variable extent, broader on sides and those of sternites even broader so to a variable extent, the entire venter sometimes tending to be yellowish and large scoop-like last sternite (or tergite) entirely yellowish; integument of thorax and scutellum above in ♂ more or less shining, duller in ♀ and covered with greyish white bloom; frons and upper parts of genae in ♂ with silvery tomentum; abdomen in ♂ also markedly and densely covered with greyish white bloom; legs with the femora yellowish brown, castaneous to dark brown, or almost black, the tibiae and tarsi, and usually the knees, in ♂ paler or even more yellowish to a variable extent, in ♀ the tibiae and at least basal halves of tarsi, and also apices of femora more consistently yellow.

Vestiture with the hairs on body and legs whitish, not very dense, but distinctly much denser and longer in ♂, those on abdomen in ♀ long only posteriorly.

Head with the eyes in ♂ in actual contact above for some distance, about 2⅓–2⅔ times as long as ocellar tubercle; frons in ♀ with the transverse depression relatively shallow, less evident than medial longitudinal one in front of tubercle; antennal joint 1 very short, as long as, or scarcely, or only a very little longer than 2; joint 3 elongate-oval, about twice as long as broad, broadest slightly beyond middle, its apical spine nearly terminal, the apex of joint scarcely produced beyond spine; palps short, inconspicuous, confined to buccal cavity; proboscis about 1,12–1,48 mm long, usually a little stouter in ♀.

Wings (cf. Fig. 2F) rather conspicuously tinted subopaquely milky whitish; veins whitish, only those in costal part slightly more yellowish or pallid; first basal cell distinctly much longer than second and much longer than part of third vein between it and second submarginal cell; second posterior cell subparallel-sided, scarcely, or not, diverging apically; apical stalk of anal cell relatively long; knobs of halteres entirely whitish in both sexes.

Legs comparatively short, the basal joint of hind tarsi distinctly much less than half length of hind tibia; claws feeble, short, mainly pale.

From 8 ♂♂ and 41 ♀♀, including the ♀ holotype and ♂ allotype, in the South African Museum.

Length of body: about 2,08–3 mm
Length of wing: about 2,4–3 mm

Distribution

Little Karoo: Oudtshoorn District (Museum expedition, October 1952) (♀ holotype and ♂ allotype); Uniondale District (Museum expedition, October 1952). Karoo: between Vondeling and Willowmore (Museum expedition, October 1952). Koup Karoo: Lammerfontein in the Moordenaars Karoo in the Laingsburg Division (Museum expedition, October 1952).

Its entirely yellow abdomen in ♀, broader yellowish hind margins of abdominal segments in ♂, the yellowish tibiae, milky whitish wings with whitish veins, and shorter proboscis distinguish it at once from *thornei* which species it appears to replace in the Little Karoo.

Apolysis lactearia sp. nov.

This species, represented by only the female sex among the new accessions, can only be confused with ♀♀ of *thornei.* The differences are however of such a nature that they cannot be considered as merely varietal. From both the typical and varietal forms of the ♀ *thornei* the ♀♀ of this new species differ as follows:

Body, including legs, almost entirely black; narrowish hind margins of tergites and only slightly broader ones of sternites pallid; narrow hind border of metapleurae also yellowish; articulating part below between tergites and sternites broadly yellowish; knees not tending to be slightly yellowish as in some ♀♀ of *thornei*; integument of body, including head, thorax above and scutellum, distinctly duller, mainly covered with greyish white bloom.

Vestiture with the hairs on body and legs distinctly very much denser and longer, more conspicuously so on abdomen, but also entirely whitish as in *thornei*.

Head with the frontal depression apparently less deep, especially that medial part of it in front of ocellar tubercle; antennal joint 3 relatively shorter, usually less than 2½ times as long as broad, its apex beyond spine distinctly very much less produced than in *thornei*, the spine more terminal and itself slightly stouter; proboscis also slender, relatively long, 2,4–2,8 mm long; palps as in *thornei* section short, inconspicuous, not projecting much.

Wings distinctly more conspicuously milky whitish; veins also pale yellowish; first basal cell also much longer than second; costal cell apparently slightly narrower, the costal vein not so markedly curved outwards as in some ♀♀ of *thornei*; second posterior cell subparallel-sided and even sightly narrowed apically as in the *thornei* section; knobs of halteres entirely whitish.

From 3 ♀♀, including the holotype, in the South African Museum.

Length of body: about 2,6–3 mm
Length of wing: about 2,8–3 mm

Distribution

North-western Karoo: Augusfontein near Calvinia (Museum expedition, September 1947).

Apolysis namaensis sp. nov.

A ♀ specimen from Namaqualand also belongs to this section and is very near *lactearia* from which it differs in the following respects:

Frons scarcely, or less, impressed in front of ocellar tubercle, less shining along the middle, being mainly dull; proboscis relatively shorter, only about 2 mm long and distinctly stouter; antennal joint 3 with the humped part nearer, or just a little beyond, middle (in *lactearia* nearer apex), the spine however very similar and also almost terminal in position; legs distinctly stouter and shorter, the femora especially are stouter, and legs with relatively longer and much denser hairs; and wings milky whitish as in *lactearia*, but with the parts of costal and first veins between apex of false vein much darker, dark brown or blackish brown, not yellowish.

Length of body: about 3 mm
Length of wing: about 3 mm

Distribution

Namaqualand: Wallekraal on road to Hondeklipbaai (Museum expedition, October 1950).

Apolysis brachycera sp. nov.

Fig. 2C

Still another ♀ specimen from the western coastal region is referable to the *thornei* and *lactearia* section, differing from both *lactearia* and *namaensis* in the following respects:

Wings, though also milky whitish, with white and not yellowish veins; antennal joint 3 (cf. Fig. 2C) distinctly very much shorter or rather more ovate, scarcely more than 1½ times as long as broad and its apical spine (even more terminal in position than in *lactearia* and *namaensis*) distinctly longer and more slender; legs distinctly much stouter and shorter, the femora being even stouter than in *namaensis* and basal joint of hind tarsi relatively shorter, distinctly much less than half length of hind tibia whereas in *lactearia* and *namaensis* it is about, or very little less than, half length of tibia; hairs on body, especially on abdomen, relatively shorter.

Length of body: about 3 mm
Length of wing: about 3 mm
Length of proboscis: about 1,88 mm

Distribution

West coastal region between Leipoldtville and Elands Bay (Museum expedition, October 1947).

Apolysis seminitens sp. nov.

Fig. 2E

This striking new species, which was also caught in the flowers of a species of *Mahernia* and which resembles the species *semiflava* superficially, however belongs to the *maherniaphila* section in which the eyes in the ♂♂ are broadly separated, the hairs on the body and legs are shorter and denser, and the legs are on the whole shorter and stouter. It is characterized as follows:

Body with the head, thorax and scutellum black, the thorax and scutellum above brilliantly shining; humeral angles and postalar calli reddish brown, especially in ♀; antennae and proboscis also sometimes reddish brown to blackish brown; abdomen and also hind margin of metapleural part in both sexes entirely very pale yellowish or pallid, the hind margins of both tergites and sternites sometimes even more broadly whitish; legs with the coxae and anterior and middle femora to beyond middle and to a variable and much lesser extent hind femora, or only outer or outer lower part of hind ones darkened yellowish brownish to dark brown or blackish brown, with the apical parts of the femora or sometimes most of the hind ones, the tibiae, and at least basal halves of tarsi very pale yellowish.

Vestiture with the fine tomentum or bloom on anterior part of frons on each side of antennae and on upper half of genae silvery greyish; hair on body and legs entirely whitish, relatively poorly developed, very short and sparse or almost absent on thorax above, that on head below, humeral angles, and across hind margin of scutellum longer, more conspicuous; that on abdomen however distinctly denser than on rest of body, much denser in ♂ than in ♀; hairs on legs much sparser and shorter than in most other species, being very short and scarcely detectable on tibiae.

Head with the eyes in ♂ broadly separated above, a little narrower than in ♀, about as wide as broad ocellar tubercle, in ♀ a little wider than tubercle; frons more deeply transversely depressed across middle in ♀ than in ♂; antennal joint 1 markedly short, transverse or bead-like, as long as, or scarcely as long as, the equally short and transverse bead-like second joint; joint 3 (cf. Fig. 2E) slightly elongate-oval to ovate, about $1\frac{3}{4}$ to twice as long as broad, broadest slightly beyond middle, its spine subterminal, quite half as long as broadest part of joint; proboscis about 1–1,4 mm long, slightly stouter in ♀; palps short, not conspicuous.

Wings conspicuously subopaquely milky whitish; veins pallid or whitish; first basal cell very much, or markedly, longer than second, and considerably more than twice as long as part of third vein between it and second submarginal cell; second posterior cell subparallel-sided, not diverging apically; knobs of halteres entirely whitish in both sexes.

Legs comparatively short and stoutish, the femora rather stout and hind ones markedly curved outwards; basal joint of hind tarsi comparatively short, very much less than half, usually nearly or about a third, length of hind tibiae; claws markedly long and slender, more than half length of last tarsal joint.

From 10 ♂♂ and 10 ♀♀, including the ♂ holotype and ♀ allotype, in the South African Museum.

Length of body: about 1,48–3,2 mm
Length of wing: about 1,88–3,08 mm

Distribution

Southern Namaqualand: Knersvlakte (Museum expedition, October 1950) (types). West coastal region: Papendorp at mouth of Olifants River (Museum expedition, October 1950).

From the similarly-coloured *semiflava* it may at once be distinguished by the separated eyes in the ♂, the more shining and polished thorax in both sexes, the relatively longer first basal cell, almost hairless tibiae, and the more strongly developed claws.

From *maherniaphila* Hesse (1938: 859) it may at once be distinguished by the entirely yellow abdomen, yellow tibiae, relatively shorter and stouter legs, shorter proboscis, relatively longer first basal cell, and denser hairs on abdomen.

Apolysis hirtella sp. nov.

Fig. 2G

Still another bicolorous new species, with the eyes separated in the ♂ and belonging to the *maherniaphila* section, is to be added here. It is characterized as follows:

Body with the head, thorax and scutellum black, dull, but with greyish white bloom sometimes evident on sides of antennal insertions and body above; ocelli reddish or reddish brown; humeral angles and postalar calli also reddish brownish or piceous; abdomen in ♂ variable in colour, either entirely or predominantly yellowish or with tergites 1 and 2 mainly dark or with only hind margins of segments broadly yellowish or yellowish red, and sometimes with the scoop-like last sternite (or tergite) mainly dark; abdomen in ♀ more constantly entirely yellowish or pallid, but sometimes with the bases of tergites, especially in basal half, or tergites 1–4, darkened to a variable extent as in ♂; antennae, proboscis and legs dark reddish brown, blackish brown to black, the femora more consistently dark, and tibiae usually more reddish brown, with the knees however yellowish.

Vestiture with the hairs on body and legs conspicuous, comparatively dense and long in comparison with many other species, denser and longer in ♂, especially on abdomen where they are characteristically erect and recurved forwards, entirely or predominantly silvery whitish, though those on abdomen in ♀ sometimes with a slight sericeous yellowish tint.

Head with the eyes in ♂ broadly separated above, on vertex even slightly wider than distance between outer margins of posterior ocelli, but slightly narrower than in ♀; transverse depression on frons slightly deeper and more evident in ♀; antennal joint 1 (cf. Fig. 2G) short, but distinctly longer than the very short second joint, sometimes nearly or about twice as long; joint 3 slightly elongate, elongate–oval to oval, about 1½ to 2 times as long as broad, at broadest part usually a little beyond middle, its apex rotundately rounded, projecting a little beyond dorsal spine which is more subapical and markedly short and feeble; proboscis about 1,44–2,2 mm long; palps small, inconspicuous.

Wings, relative to body, long, distinctly tinted milky whitish; veins mainly pallid or pale yellowish, more whitish in hinder and basal half, the costal vein beyond apex of false vein to apex of wing and even round posteriorly to second posterior cell and sometimes also apical parts of posterior veins in this region darkened or markedly dark; costal cell markedly broad and outwardly curved at level of cross vein; first basal cell longer than second and distinctly longer than part of third vein between it and second submarginal cell; second posterior cell subparallel-sided; knobs of halteres entirely pallid or whitish, but sometimes with an indication of a dark spot above in some ♂♂.

Legs rather short and stoutish, the femora rather thick; basal joint of hind tarsi short, only about a third length of hind tibiae; claws short but strong.

From 6 ♂♂ and 6 ♀♀, including the ♂ holotype and ♀ allotype, in the South African Museum.

Length of body: about 1,8–2,72 mm
Length of wing: about 2,56–3,08 mm

Distribution

Koup Karoo (labelled Gouph): Laingsburg District (Museum staff, February 1938) (types); Lammerfontein in the Moordenaars Karoo near Laingsburg (Museum expedition, October 1952).

Easily recognized by its rather dense vestiture, erect and recurved hairs on abdomen of ♂, mainly yellowish abdomen, and stoutish legs, in which respects it also differs from *maherniaphila*.

From *semiflava* and *seminitens*, which also have a mainly or entirely yellowish abdomen, it differs in being distinctly more hairy, and from the former species in the separated eyes in the ♂, and from the latter in being more hairy, in not having a smooth and shining front part of the body, entirely dark or black legs, etc.

REVISED KEY TO THE KNOWN SOUTH AFRICAN SPECIES OF *Apolysis*

1 (*a*) First basal (cf. Fig. 2D) cell in wings as long as, or scarcely, or only a little longer than second, and as long as, or subequal to, or sometimes even shorter than, part of third vein between it and apical cell (if longer first basal cell only slightly longer than second); second posterior cell widely divergent apically; wings rarely with a very distinct milky whitish tint (if so first basal cell not long); palps usually elongate, conspicuously projecting (if short other characters do not differ) 2

(*b*) First basal cell (cf. Fig. 2F) distinctly much longer than second and distinctly much longer than part of third vein between it and apical cell; second posterior cell subparallel-sided, sometimes even slightly narrowed apically; wings usually with a more distinct, sometimes conspicuous, milky whitish tint; palps usually much shorter, or very short and insignificant 12

2 (*a*) Palps longer or elongate, conspicuously visible, projecting much beyond buccal cavity; antennal joint 3 distinctly longer, more elongate, much more than 2,5 times as long as broad and usually equally long or broad in both sexes; wings more elongate, relatively narrower, cinereous hyaline, cinereous, or even distinctly dusky or infuscated, the veins distinctly darker; larger forms, usually much more than 2 or 2,5 mm long 3

(*b*) Palps much shorter or very short, insignificant, not easily visible, either hidden in buccal cavity or not conspicuously projecting; antennal joint 3 distinctly relatively shorter, more oval or ovate, or not much more than 2 or 2,5 times as long as broad and either shorter or broader and more distinctly ovate in ♀♀; wings relatively shorter and broader, clear hyaline or with a faint or distinct milky whitish tint, the veins paler, more yellowish; smaller or minute forms, usually less than 2 or 2,5 mm long.. 10

3 (*a*) Hairs on head, occiput and genae, on thorax and scutellum above either entirely pale or whitish like rest of hairs on body and legs, or with fewer dark ones and then not on all the parts mentioned; wings clearer or only faintly greyish hyaline and with a more milky whitish subopacity in certain lights; apical part of antennal joint 3 beyond spine-like process slightly, but distinctly, more produced or apical margin above, just beyond spine, distinctly more indented or incised 4

(*b*) Hairs on head, occiput and sometimes genae and on thorax above and scutellum distinctly not white, darker or black, or with more numerous dark ones; wings darker, distinctly more cinereous, dusky or infuscated, the subopacity more greyish than whitish; apical part of antennal joint 3 beyond spine usually less produced, more rotundately rounded, the apical margin above, just beyond spine, usually less incised 11

4 (*a*) Abdomen with the hind margins of tergites and sternites broader, more conspicuously, yellowish or pallid, or the venter itself may be mainly yellowish; antennal joint 3 with the prominence on dorsal margin, just before subapical excavation, less sharply or angularly prominent, the joint thus less humped in appearance 5

(*b*) Abdomen with the hind margins of the tergites and sternites only very narrowly or obscurely pallid or yellowish, greater part of venter not mainly yellowish; antennal joint 3 with the prominence, just before apical excavation, distinctly more sharply or angularly prominent, giving joint a more humped appearance 10

5 (*a*) Body above, especially abdomen, dull, not shining; hind margins of tergites less broadly pallid or yellowish; sternites in some ♀♀, and sometimes in some ♂♂ also, more broadly yellowish or even entire venter yellowish; hairs on body more whitish or entirely sericeous whitish; proboscis on the whole relatively shorter, stouter, usually only about 0,6–1 mm long 6

(*b*) Body above, especially abdomen above, distinctly more shining; hind margins of tergites more broadly, more conspicuously, ivory yellowish or yellowish; greater discal part of venter, even in ♀♀, not conspicuously yellowish; hairs on occiput, thorax above or only basally, and on scutellum, and sometimes on abdomen above to a certain extent, distinctly more yellowish or even darker, not whitish; proboscis relatively longer, usually about 1–2 mm 8

6 (*a*) Legs distinctly paler, more reddish brown, the tibiae and tarsi even paler; entire venter, even in ♂, distinctly yellowish; hairs on body distinctly denser, more shaggy; wings relatively shorter, the veins paler, more yellowish brown; second submarginal cell relatively short, shorter than part of third vein between it and first basal cell; proboscis about 1,33 mm long .. .. ♂ *xanthogaster* Hesse

(*b*) Legs on the whole darker or entirely black; entire venter in known ♂♂ not yellowish; hairs on body distinctly less dense, sparser; wings more elongate, the veins darker brown to dark brown; second submarginal cell normally long, subequal in length to, or even slightly longer than, part of third vein between it and first basal cell; proboscis relatively shorter, about 0,6–1 mm long 7

7 (*a*) Wings more greyish hyaline; hind margins of sternites in ♀ more broadly yellowish, even entire venter yellowish; antennal joint 1 distinctly longer than joint 2; palps more slender, relatively longer, distinctly longer than antennal joint 3; interocular space in ♀, at narrowest part, on vertex relatively narrower, subequal to length of antennal joint 3; knobs of halteres in ♀ entirely whitish .. .. ♀ ***monticola*** sp. nov.

(*b*) Wings more distinctly tinted subopaquely milky whitish; hind margins of sternites apparently less broadly yellowish, the entire venter not yellowish; antennal joint 1 markedly short, subequal in length to, or very little longer than, 2; palps shorter, stouter, relatively shorter, subequal in length to, or scarcely longer than, antennal joint 3; interocular space on vertex in ♀ relatively broader, distinctly broader than length of antennal joint 3; knobs of halteres either entirely whitish or slightly darkened above in ♀, consistently darkened above in ♂ .... ♂ ♀ ***capicola*** sp. nov. (more especially some ♀♀)

8 (*a*) Rim of buccal cavity ivory yellowish; hind margins of tergites more broadly ivory yellowish; knees slightly yellowish and tibiae and tarsi tending to be less dark than femora; hairs on occiput and thorax above more straw-coloured yellowish; knobs of halteres slightly darkened above towards base; proboscis slightly longer, about 2 mm long; antennal joint 1 slightly longer, longer than 2; slightly larger form, about 3,5 mm long, with a wing-length of about 4 mm .. .... ♀ *cingulata* Hesse

(*b*) Rim of buccal cavity dark or dark reddish brown; hind margins of tergites only very narrowly ivory yellowish; legs, including knees, entirely dark or black; hairs on occiput and thorax anteriorly whitish, those on base of thorax above and on scutellum dark or blackish; knobs of halteres entirely pale yellowish white above; proboscis shorter, only about 1 mm long; antennal joint 1 shorter, scarcely longer than 2; smaller form, about 2,2 mm long, with a wing-length of about 2,4 mm ♀ ***thamnophila*** sp. nov.

9 (*a*) Antennal joint 1 much longer, at least twice length of 2; prominence in front of subapical excavation on joint 3 above more angularly prominent; proboscis distinctly more slender, thinner; palps more slender, longer than antennal joint 3; wings more greyish hyaline, not or scarcely tinted faintly milky whitish, the veins darker brownish to blackish brown; hind margins of tergites and sternites in both sexes narrowly, or scarcely, pallid; knobs of halteres in ♀♀ usually entirely white .. 10

(*b*) Antennal joint 1 markedly short, about as long as, or only a very little longer than, 2; prominence on dorsum of joint 3 less angularly prominent; proboscis distinctly stouter, appearing shorter; palps relatively shorter and stouter, shorter, or at least not much longer, than antennal joint 3; wings distinctly tinted more subopaquely whitish, the veins more yellowish brown; hind margins of tergites and sternites in some ♀♀ relatively more broadly yellowish; knobs of halteres in some ♀♀ darkened above as in ♂♂ .. .. ♂♀ *capicola* sp. nov.

10 (*a*) Smaller species, about 1,8–2 mm long, with a wing-length of about 2,12–2,4 mm; wings faintly more greyish or cinereous, more so in ♂, the veins darker, dark brownish to blackish brown; apical stalk of anal cell relatively longer, usually a little longer than apical cross vein of second basal cell; narrow pallid hind margins of tergites and sternites, even in ♀, tending to be less constant, more obscure; hairs on body and legs shorter, sparser, and fine ones on hind tibiae relatively shorter, less conspicuous .. .. ♂ ♀ *stuckenbergi* sp. nov.

(*b*) Slightly larger species, about 2,4–3 mm long, with a wing-length of about 3–3,2 mm; wings less greyish, with a more distinct whitish subopacity, the veins slightly paler, more yellowish brown; apical stalk of anal cell relatively shorter, subequal to, or even shorter than, apical cross vein of second basal cell; narrow pallid hind margins of tergites and sternites, in ♀ at least, more constantly present, especially the more broadish ones on sternites; hairs on body and legs longer, slightly darker, and fine hairs on hind tibiae relatively longer, more conspicuous
♀ *oreophila* sp. nov.

11 (*a*) Wings clearer, less dusky or infuscated, only greyish hyaline or tinted slightly cinereous, the veins more reddish brown; part of third vein between first basal cell and apical cell tending to be longer, subequal to, or only a little shorter than, latter cell; knobs of halteres in ♂ darkened above only; hind margins of tergites and sternites in both sexes less conspicuously, or broadly, yellowish, only narrowly or obscurely pallid; hairs on body less extensively dark or black, those on head below, on abdomen, and on legs, even in ♂, paler or more whitish; hump before apical excavation on antennal joint 3 less prominent .. .. ♂ ♀ *humilis* Loew

(*b*) Wings distinctly dusky, more infuscated, or smoky brownish, even more so in ♂, the veins darker, very dark brown, blackish brown, or even black; part of third vein between first basal cell and apical cell tending to be markedly shorter than apical cell; knobs of halteres in ♂ usually darkened above and below; hind margins of tergites and sternites, in ♀ especially, more conspicuously yellowish and even more broadly so on venter; hairs on body more extensively dark or black, those on head below, on abdomen and legs in ♂ tending to be black, in ♀ more yellowish, yellowish brown to brown (if paler other characters do not differ); hump before apical excavation on antennal joint 3 more prominent or even knob-like
♂ ♀ *fumalis* Hesse

12 (*a*) Slightly larger, more bulky species, about 1,5–2,5 mm long, with a wing-length of about 1,5–2,5 mm; body duller, with more conspicuous, denser, greyish white bloom, in ♀ especially, with two rows of velvety black quadrangular patches on abdomen above (those on tergites 2 and 3 the largest), and with black patches on thorax; proboscis much shorter, stouter, only about 0,4–0,6 mm long; wings more conspicuously milky whitish, their first basal cell distinctly longer than part of third vein between it and apical cell and latter also considerably longer than this part; apical stalk of anal cell shorter, less than twice width of base of third posterior cell; hairs on body and legs much denser, longer, markedly so in ♀; eyes in ♂ in actual contact for some distance in front of ocellar tubercle. . ♂ ♀ *brevirostris* Hesse

(*b*) Very much smaller, or minute, less bulky species, only about 1,2–1,7 mm long, with a wing-length of about 1,5–1,9 mm; body either less dull and with much feebler greyish bloom, or smooth and shining, without any bloom, without any distinct, conspicuous, black, velvety patches on abdomen; proboscis, relative to body, much longer, more slender, about 0,68–1,5 mm; wings tinted more faintly milky whitish, the first basal cell distinctly shorter than, or only subequal in length to, part of vein between it and apical cell, and latter sub-equal in length to, or even shorter than, same part; apical stalk of anal cell longer, quite or at least twice length of base of third posterior cell; hairs on body and legs either much sparser and shorter, or very sparse and short; eyes in known ♂♂ broadly separated, only a little narrower than in ♀♀ 13

13 (*a*) Head and body smooth, shining, polished, without any greyish tomentum; hind margins of tergites and sternites, especially in ♀, more broadly and more conspicuously yellowish; hairs on head, body and legs minute or absent in ♀, very sparse and short on thorax and abdomen in ♂; legs shorter, the tarsi shorter and basal joint of hind ones much shorter than half length of hind tibia; veins in hinder part of wings paler yellowish or becoming paler distally; hind margin and microtrichial hairs in wings very pale or whitish; first basal cell as long as second; anterior part of frons distinctly more convex or subtumid; proboscis in ♀ slightly less stout, reaching the length of 1,9 mm .. .. ♂ ♀ *minuscula* sp. nov.

(*b*) Head and body more dulled to a variable extent by fine greyish tomentum; hind margins of tergites and sternites, even in ♀, only narrowly, scarcely, or obscurely, pallid or yellowish; hairs on head and body, especially abdomen and legs, even in ♀, distinctly denser and longer, those on hind tibiae distinctly longer, more evident; legs relatively longer, the tarsi longer, and basal joint of hind ones quite or nearly half length of hind tibia; veins in wings darker; hind margin of wings and microtrichial fringe dark; first basal cell slightly longer than second; frons anteriorly less convex; proboscis, even in ♀, rather stoutish and short, only about 0,68 mm long ♀ *lindneri* Hesse

14 (*a*) Eyes in ♂♂ in actual contact above for some distance, about 2½ to nearly 3 times length of ocellar tubercle, and with the upper facets distinctly much coarser than lower ones; distance between posterior ocelli in ♀♀ subequal to, as long as, or scarcely perceptibly longer than, distance between them and inner margin of eyes; vestiture on body and legs usually longer, even if sparse, and that on abdomen, especially in ♀♀, sometimes tending to be less dense; legs on the whole more slender, longer, the basal joint of hind tarsi usually relatively longer, at least half length of hind tibiae .. 15

(*b*) Eyes in ♂♂ widely separated above by a broad space which is only a little narrower than that of ♀♀, and with the upper facets not coarser than lower ones; distance between posterior ocelli in ♀♀ distinctly or perceptibly longer than distance between them and inner margin of eyes; vestiture on body and legs on the whole shorter, usually denser, and that on abdomen, especially in ♀♀, usually markedly denser; legs on the whole shorter, stouter, the basal joint of hind tarsi usually shorter, much shorter than half length of hind tibiae 21

15 (*a*) Legs either entirely dark or black or, if tibiae and tarsi are paler, they are not pallid or pale yellowish; yellow on abdomen distinctly less developed, the hind margins of tergites and sternites in known ♂♂ either not yellowish or pallid or only narrowly, obscurely and less conspicuously so, and in ♀♀ abdomen is not entirely or predominantly yellowish, at most with only broadish pallid or yellowish hind margins; wings slightly less conspicuously milky whitish and, if so, veins tend to be more yellowish than whitish or pallid and, if whitish, legs are dark; proboscis relatively longer, usually more than 1,5 mm 16

(*b*) Legs on the whole much paler, the femora more yellowish brownish or brownish and greater part of tibiae and tarsi, excluding only the brownish apical parts of latter and sometimes slightly brownish apices of tibiae, entirely or predominantly pale yellowish; yellow on abdomen more developed, the entire or greater part of abdomen in ♀ very pale yellowish or pallid, and in ♂ with broader pallid or yellowish hind margins, sometimes very broad on sides, and with last elongated sternite entirely or predominantly yellowish or at least with much yellowish; wings more conspicuously subopaquely milky whitish, the veins very pallid or whitish; proboscis relatively short, only about 1,12–1,48 mm long .. ♂ ♀ *semiflava* sp. nov.

16 (*a*) Integument of body above, especially thorax and scutellum, and in ♀ also entire or greater part of frons, more shining, less dull, not densely covered with greyish white bloom; antennal joint 3 more elongate, relatively longer, about 2,5–3 times as long as broad, its apex beyond subapical spine distinctly, though slightly, more produced, more rounded, the spine thus distinctly more subapical in position; frontal depression in ♀♀ relatively deeper and medial part in front of anterior ocellus also distinctly deeper; wings either not distinctly milky whitish or tinted less so; hairs on body and legs, especially on abdomen, and more so in ♀♀, distinctly shorter and sparser 17

(*b*) Integument of body above and in ♀ also greater part of frons distinctly duller, very densely covered with greyish white bloom; antennal joint 3 less elongate, shorter, not more than, usually less than, 2 times as long as broad, its apex beyond spine distinctly not produced, the spine appearing more terminal; frontal depression in ♀♀ less deep, especially the medial part in front of anterior ocellus; wings more conspicuously subopaquely milky whitish; hairs on body and legs, especially on abdomen, even in ♀♀, distinctly longer, more shaggy and relatively denser .. 19

17 (*a*) Wings with a distinct, though faint, milky whitish tint; costal cell relatively broad at middle, its anterior margin more curved outwards near cross vein; knobs of halteres in ♂♂ usually either entirely dark above or darkened above to a variable extent; abdomen in ♀♀ with the hind margins of tergites and sternites yellowish to a variable extent, more so apically; anterior part or half of frons, genae, and abdomen above in ♀♀ distinctly duller .. .. ♂ ♀ *thornei* Hesse (and forms of it)

(*b*) Wings more vitreous hyaline, without any perceptible milky whitish tint; costal cell appearing narrower, its anterior margin not markedly curved outwards; knobs of halteres, in known ♂♂, entirely whitish or pallid; abdomen in known ♀♀ entirely black or with scarcely any indication of yellowish hind margins; entire frons and body above in ♀♀ shining .. a distinct ♀ form of *thornei* Hesse and some ♂♂ (18)

18 (*a*) Base of wings up to cross vein in costal cell more subopaquely whitish
♂ form of *thornei* Hesse

(*b*) Base of wings up to cross vein distinctly more opaquely yellowish
♂ form of *thornei* Hesse

19 (*a*) Veins in wings distinctly more yellowish; antennal joint 3 distinctly more elongate, at least twice as long as broad, its apical spine relatively stouter and shorter; legs relatively longer, the basal joint of hind tarsi longer, only a little less than, or nearly, half length of hind tibiae; hairs on abdomen relatively longer 20

(*b*) Veins in wings white or whitish; antennal joint 3 distinctly shorter, more ovate, scarcely more than 1,5 times as long as broad, its apical spine distinctly more slender and longer; legs relatively stouter and shorter, the basal joint of hind tarsi shorter, distinctly much less than half length of hind tibiae; hairs on abdomen relatively shorter .. .. ♀ *brachycera* sp. nov.

20 (*a*) Frons more distinctly and more deeply depressed in front of ocellar tubercle, also more shining along middle; proboscis slightly longer, more slender, about 2,48–2,9 mm long; humped part of antennal joint 3 nearer apex; legs distinctly more slender, longer, the femora more slender, with relatively shorter hairs; part of costal vein and first main vein beyond apex of false vein yellow or more yellowish, the costal vein only slightly darkened apically .. .. ♀ *lactearia* sp. nov.

(*b*) Frons scarcely or less impressed in front of tubercle, less shining along middle, mainly dull; proboscis distinctly shorter and stouter, only about 2 mm long; humped part of antennal joint 3 nearer, or just a little beyond, middle; legs distinctly shorter and stouter, the femora distinctly stouter, with relatively longer hairs; part of costal vein and first vein, beyond apex of false vein, much darker, dark brown or blackish brown .. .. ♀ *namaensis* sp. nov.

21 (*a*) Abdomen not predominantly or entirely yellowish or pallid in both sexes, only hind margins of tergites and sternites being yellowish to a variable extent, much less so, or only narrowly so, in ♂; legs distinctly longer, more slender, the femora relatively less stout, and basal joint of hind tarsi relatively longer, about, or a little less than, or even a little more than, half length of hind tibiae; proboscis on the whole longer, reaching up to 2 mm; hairs on abdomen, even in ♂, sparser ♂ ♀ *maherniaphila* Hesse

(*b*) Abdomen predominantly or entirely pallid or yellowish, or with broader yellowish hind margins, in ♂♂, and entirely so in ♀♀; legs distinctly shorter, stouter, the femora relatively thicker and stouter, and basal joint of hind tarsi shorter, usually very much less than half length of hind tibiae; proboscis on the whole shorter, less than 2 mm; hairs on abdomen, even in ♀♀, denser, sometimes markedly dense and conspicuous 22

22 (*a*) Integument of head above, thorax, and scutellum brilliantly shining, smooth and polished in appearance; hairs on body and legs, especially on thorax and scutellum, less developed, sparser, those on abdomen not so markedly recurved forwards; abdomen in both sexes entirely pallid or very pale yellowish; legs with more yellowish, sometimes mainly yellowish or with at least apical parts or halves of femora, entire tibiae, and basal halves of tarsi pale yellowish, and the hind femora tending to be more curved; antennal joint 1 very short, not or scarcely as long as second; antennal joint 3 more narrowed basally, its spine much longer and more apically situated; costal cell less markedly broad, its anterior vein not so convexly arched; first basal cell relatively longer .. .. ♂ ♀ *seminitens* sp. nov.

(*b*) Integument of head above, thorax, and scutellum dull, densely covered with greyish white bloom; hairs on body and legs, even on thorax above, distinctly markedly denser, those on abdomen above, especially in ♂, markedly upright or recurved forwards; abdomen in ♂ sometimes with the bases of tergites darkened to a variable extent and in ♀ sometimes with only hind margins of sternites yellowish to a variable extent; legs mainly or entirely dark, dark castaneous brown to black, only the knees yellowish, and with the hind femora less markedly curved; antennal joint 1 a little or distinctly longer than 2; antennal joint 3 on the whole broader, less narrowed basally, its apical spine much feebler, more dorsal or subapical in position; costal cell broader, more markedly dilated, its anterior vein convexly arched; first basal cell relatively shorter .. .. ♂ ♀ *hirtella* sp. nov.

Genus *Oligodranes* Loew

Oligodranes: Hesse, 1938: 861. Hull, 1973: 219.

As is stated under the subfamily Usiinae in this paper the genus *Oligodranes* is the other genus, formerly placed in the subfamily Phthiriinae, which Hull, in his recent monograph of the genera of the Bombyliidae, transferred to the subfamily Usiinae.

In view of the discovery of four additional South African species of this genus, which I take to be the South African counterpart of the Palaearctic form and of which I gave a supplementary description in 1938 based solely on the South African representatives, the following supplementary notes on the genus should now be added:

The South African forms seem to show distinct colour differentiation in the two sexes. All the known ♂♂ are consistent in being predominantly or entirely black; the yellow colouring on body and legs being much reduced or almost absent. The ♀♀ on the other hand always show more extensive yellow colouring or a striking pattern of yellow or pallid markings on the head, thorax, pleurae, and abdomen.

As far as cephalic characters are concerned it is to be noted that the eyes in ♂♂ are not always in contact above; these in some species are widely separated as in the case of the ♀♀. In this respect they agree with ♂♂ of some species in the genus *Apolysis*. In the latter genus however the last tergite (or sternite) in the ♂♂ is scoop-like and the genitalia are prominent, thus rendering differentiation between the sexes easy. In *Oligodranes* the genitalia of the ♂♂ are very small, insignificant, usually hidden or not easily seen. Confusion of the sexes is therefore not excluded if the eyes of the ♂ are broadly separated as in the ♀. Such a mistake was made by me in 1938 in the case of the supposed ♀ of *namaensis* Hesse (see below).

As in the case of species of *Apolysis* most of the South African representatives of *Oligodranes* frequent flowers and in the latter case mostly those of species of *Mesembryanthemum.*

Oligodranes namaensis Hesse

Oligodranes namaensis Hesse, 1938: 864, fig. 263b.

Since my description of this species in 1938 the Museum has acquired a long series of both sexes of this species. As they were caught together frequenting the flowers of species of *Mesembryanthemum* and also show certain characters in common there can be no doubt that the sexes belong to the same species.

This discovery necessitates the correction of an error in identification made by me in 1938. A comparison of the real ♀ of *namaensis* with the supposed ♀ allotype of *namaensis* has not only shown that the latter is not the ♀ of *namaensis,* but that it is a ♂ with separated eyes belonging to another species which is described below as a new species. Only the characters given for the ♂ specimen of *namaensis* are therefore valid in my description of 1938. A supplementary redescription of this species, which also includes the real and differently-coloured ♀, is given here to render its recognition more easy:

Body and legs in ♂ mainly black, with the frons in front to a variable extent, palps, humeral angles and anterior spiracular area to a variable extent, an infusion just below base of wings, postalar calli to a variable extent, metapleural part just below halteres, ligamentous connection between squama and scutellum, very narrow hind margins of tergites and broader ones of sternites pallid or yellowish; knees of ♂ usually also yellowish.

Body in ♀ also partly black, but with the following parts very pale yellow: sides of frons in middle, anterior part of frons, entire genae, palps, greater part of head below, occiput broadly behind eyes (except broadish, black, central, postvertical stripe and middle part of occiput), triangular humeral spot, a broad spot just below it, notopleural part, postalar calli broadly, broadish base of thorax (or two spots), entire scutellum, propleural spot, anterior spiracular part, prosternal part, area just below wing-bases, a longitudinal fascia along middle of pleurae, greater part of metapleural region, fairly broadish hind margins of tergites, broader hind margins of sternites or sometimes almost entire venter, entire coxae (excepting only a brownish anterior basal spot on hind ones), and the femora (excepting only the brownish anterior upper surfaces, or spots, in apical halves, especially of hind ones).

Vestiture with the hairs sparse, longer in ♂, shorter and denser on abdomen in ♀, entirely pale or whitish, though with slight sericeous yellowish gleams on abdomen in ♀.

Head with the eyes above in ♂ in actual contact for a distance at least twice length of ocellar tubercle; interocular space on vertex in ♀ quite twice width of ocellar tubercle; transverse depression across middle of frons in ♀ rather deep and conspicuous; antennal joint 1 about 1½–2 times length of joint 2; joint 3 about 1⅔–2 times combined length of joints 1 and 2; proboscis 1,12–1,4 (average 1,2) mm long; palps slender, subequal in length to, or about as long as, antennal joint 3.

Wings hyaline, iridescent, with a very feeble milky whitish tint in certain lights, more detectable at base; veins yellowish brown to brown, more yellowish at base; middle cross vein at about between basal third and basal fourth of discoidal cell; first basal cell usually a little shorter than distance of third vein between it and base of second submarginal cell and latter cell, along lower vein, also distinctly shorter than this part of third vein; knobs of halteres entirely pallid or whitish in both sexes.

Hypopygium of ♂ as shown in figure 263b (Hesse 1938: 864).

From 12 ♂♂ (including original ♂ holotype) and 34 ♀♀.

Length of body: about 1,88–2,28 mm
Length of wing: about 2,2–2,6 mm

Distribution

Namaqualand: Kamieskroon (Museum staff, September 1930) (♂ holotype). Bushmanland: Aggenys between Springbok and Pella (Museum staff, October 1939) (♂♂, ♀ allotype and ♀ paratypes). West coastal region: Citrusdal District (Museum expedition, November 1948) (♂♂).

Oligodranes triseriatellus sp. nov.

Fig. 3A, C

This slightly variable species, which was also caught on the flowers of a species of *Mesembryanthemum*, is very near *namaensis*. From the latter it however differs in the following respects:

Body in ♂ with the hind margins of tergites and sternites distinctly much more broadly and more conspicuously yellow, sometimes extensively so; body in ♀ with the distribution of black and yellow variable, differing from ♀ of *namaensis* in having the entire occiput behind ocellar tubercle and entire frons (excepting sometimes for a much narrower median dark spot or line about middle) yellow, sides and base of thorax above distinctly much more broadly and extensively yellow, the part on each side above wing-base also continuously yellow, isolating a rather conspicuous, round, black spot or peninsula on each side, in having the pleurae more extensively yellow (sometimes with only a large black spot in upper half of mesopleuron), with the yellow on abdomen above much more extensive than in *namaensis*, the hind margins very broadly

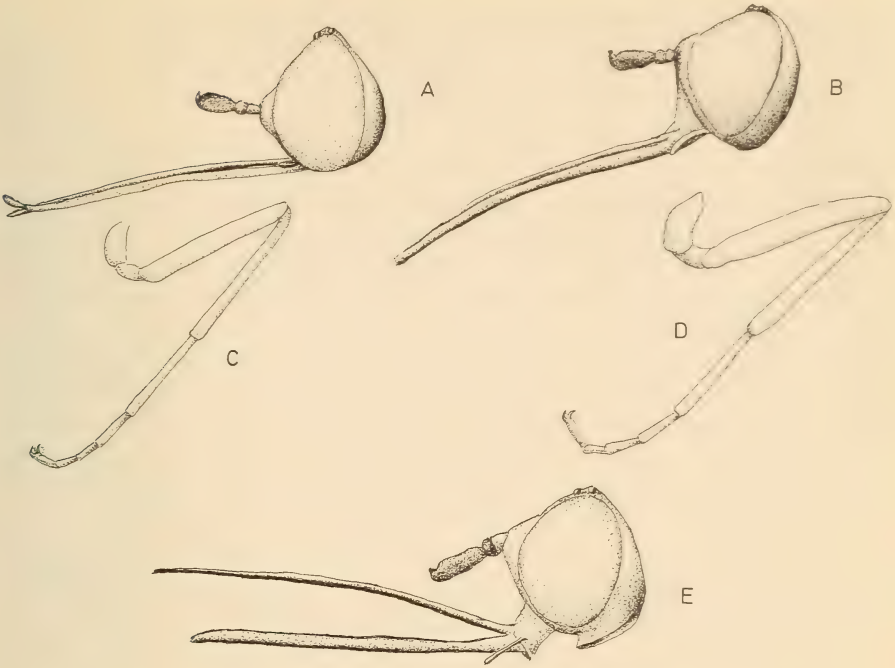

Fig. 3. Left side views of heads and left hind legs of some new species of *Oligodranes*. (All to the same scale.)
A. ♂ *triseriatellus;* B. ♂ *anomalus;* C. ♂ *triseriatellus;* D. ♂ *anomalus;* E. ♀ *puberulus.*

so, reducing or more often breaking up the black basal parts of tergites into three longitudinal rows of black spots or patches which become smaller posteriorly and which, in some specimens, are even absent in posterior half of abdomen or very much reduced in size, almost the entire abdomen being yellowish; legs in ♀ often also with more yellowish on the tibiae or on middle of tibeae, especially hind ones, and with the brownish infusions on upper or anterior parts of femora in apical halves usually also more conspicuous.

Head (cf. Fig. 3A) with antennal joint 1 tending to be partly yellowish in ♂ and entirely yellowish in ♀; proboscis on the whole comparatively longer, 1,2–1,8 mm; palps also shorter, usually even less conspicuous, usually distinctly shorter than antennal joint 3.

Wings with the veins on the whole paler, more yellowish; distance between middle cross vein and base of second submarginal cell relatively shorter, especially in ♂, usually only a little, or scarcely, longer than lower vein of cell itself whereas in *namaensis* this distance is more constantly markedly longer; middle cross vein with a tendency to be farther away, at least at, or slightly more than, basal third of discoidal cell.

Legs with the left hind one of ♂ shown in Figure 3C.

From 4 ♂♂ and 15 ♀♀, including the types, in the South African Museum.

Length of body: about 1,72–3,28 mm
Length of wing: about 2,12–3,68 mm

Distribution

Bushmanland: Pofadder (Museum staff, October 1939) (types and paratypes); Aggenys between Springbok and Pella (Museum staff, October 1939) (paratypes). North-western Cape: Putsonderwater (Museum staff, October 1939) (paratypes). Great Karoo: Richmond District (Museum staff, November 1939) (♀ paratype).

As is evident from the description this species appears to be variable not only in size, but also in the extent of the yellowish or black colouring on the head, abdomen and legs in ♀♀. Some ♀♀ have the three rows of black spots on the abdomen less isolated or larger, tending to coalesce into black basal bands across the tergites; in others the spots are small and the tibiae yellowish to a variable extent, sometimes almost entirely yellowish.

The ♀ paratype from Richmond has not only a tendency for the three series of black basal spots on tergites 1–3 to coalesce but also to have a dark medial postvertical stripe on the occiput as in ♀ of *namaensis*.

Oligodranes puberulus sp. nov.

Fig. 3E

Another new species caught on flowers of a species of *Mesembryanthemum* is characterized as follows:

Body and legs mainly black in both sexes, but in ♂ with the frons in front and upper half of genae, palps, humeral angle, margins of anterior spiracle, notopleural ridge, area just below wing-bases, postalar calli, ligamentous connection between squama and scutellum, metapleural part just below halteres, and narrow hind margins of tergites and sternites pale yellowish or pallid, the hind margins of tergites being more whitish; the following parts in ♀ are very pale yellowish or pallid; front part or half of frons, genae, palps, head below anteriorly and continuous broadly to halfway up on each side behind eyes, humeral tubercle and anterior spiracular area, notopleural ridge, more extensive area below wing-basis, postalar calli, ligamentous connection, hind border of scutellum, hind margins of tergites (slightly broader than in ♂) and broader hind margins of sternites, prosternal part to a variable extent, propleural part just above front coxae, a longitudinal band along middle of pleurae, and greater part of metapleural region in front of and below halteres; knees in ♂ yellowish red and in ♀ more yellowish as well as apices of coxae, especially front ones; integument of body dull, with greyish bloom, espeically in ♂.

Vestiture with the hairs longer and much denser than in *namaensis*, longer in ♂ than in ♀, entirely silvery whitish.

Head (cf. Fig. 3E) with the eyes in ♂ in contact above for a distance about 2⅓ times length of ocellar tubercle, the line of contact rather deeply impressed and facets in upper half of eyes rather coarse; interocular space on vertex in ♀ about twice width of ocellar tubercle; transverse frontal depression in ♀ deep and distinct; antennal joint 1 about 1½–2 times length of small transverse joint 2; joint 3 at least twice length of joints 1 and 2 combined, subparallel-sided, its dorsal subapical spine short and rather stoutish; palps appearing rather long, conspicuously visible, almost, or about, as long as antennal join 3; proboscis about 1,4–1,68 mm long.

Wings vitrous hyaline, iridescent; veins yellowish; middle cross vein at about, or a little more than, a third of discoidal cell; part of third vein between middle cross vein and second submarginal cell distinctly shorter than length of latter cell; knobs of halteres entirely whitish, pallid, or yellowish in both sexes.

From 2 ♂♂ and 2 ♀♀, including the type specimens, in the South African Museum.

Length of body: about 2,6–3,08 mm
Length of wing: about 2,88–3,4 mm

Distribution

Bushmanland: Aggenys between Springbok and Pella (Museum staff, October 1939) (types); Pofadder (Museum staff, October 1939).

From both *namaensis* and *triseriatellus* this species may at once be distinguished by the much denser and longer vestiture, the relatively more conspicuous and longer palps, the comparatively longer second submarginal cell in relation to part of third vein between it and middle cross vein, the position of the latter cross vein, and in ♀ the less extensive yellow markings on head and body.

Oligodranes flavifemoris sp. nov.

This species resembles *puberulus* very closely, but differs from it in the following respects:

Body with the integument of the frontal triangle, sides of face and upper parts of genae in ♂ entirely dark, not yellowish, but covered with pale or greyish white bloom; head below in ♀ slightly more extensively yellowish; hind margins of tergites in ♀ distinctly more broadly pallid or yellowish, sometimes occupying nearly half of tergites posteriorly; hind margins of sternites in both sexes distinctly very much more broadly yellowish, the entire venter in some ♀♀ sometimes tending to be yellowish; legs with the coxae and femora in ♀ mainly and conspicuously yellow, not black as in ♀ *puberulus*, only the upper or anterior surfaces in apical halves of at least front and hind femora darkened or brownish to a variable extent as in ♀♀ of *namaensis*.

Vestiture as dense as in *puberulus*.

Head with antennal joint 1 apparently a little longer, especially in ♀, quite 2½ times as long as small transverse joint 2; proboscis about 1,2–1,66 mm long.

Wings, even though faintly tinted milky whitish, distinctly more so than in *puberulus*; veins slightly darker, more brownish; knobs of halteres in ♂ darkened above.

From 1 ♂ and 8 ♀♀, including the types, in the South African Museum.

Length of body: about 2,32–3,64 mm
Length of wing: about 2,6–3,6 mm

Distribution

Southern coastal region: Pearly Beach in the Bredasdorp District (Museum staff, December 1958) (types). Koup Karoo: Laingsburg District (Museum staff, February 1938). West coastal region (Olifants River Valley): Bulhoek between Clanwilliam and Klawer (Museum expedition, October 1950).

Oligodranes anomalus sp. nov.

Fig. 3B, D

Oligodranes namaensis (described as ♀) Hesse, 1938: 864, fig. 263a (n. syn.).

As has been stated in my supplementary redescription of *namaensis* in this paper, the discovery of the real ♀ of the latter species eliminates the specimen described by me in 1938 as the ♀ of *namaensis*. This specimen moreover is not a ♀ but a ♂ in which the eyes are broadly separated above as in ♀♀ of this genus. It belongs to a newly discovered section of *Oligodranes* in which the ♂♂ are not holoptic but dichoptic as in ♀♀ where the eyes are not in contact above but widely separated. This representative of the section by itself is characterized as follows:

Body and legs mainly black, but with the following parts pale yellowish or pallid: extreme anterior part (around antennal insertions) of frons, genae, buccal cavity, palps, humeral angles and anterior spiracular area, notopleural fold, area just below wing-bases, postalar calli and area below it, ligamentous connection between squama and scutellum, part of metapleural region below halteres, hind margin of metapleural part, narrow hind margins of tergites and sternites, and hind margin of last sternite (or tergite); coxae and legs more deep dark reddish brown than black, the apices of coxae, especially front ones, and the knees slightly paler, more yellowish reddish; integument dull.

Vestiture with the hairs on body and legs sparse, slightly denser on abdomen, entirely pale or whitish.

Head (cf. Fig. 3B) with the eyes broadly separated above, about $1\frac{3}{5}$ times width of ocellar tubercle; frons almost parallel-sided, slightly depressed centrally at about middle, not deeply and transversely as in ♀♀ of *Oligodranes*; antennal joint 1 (cf. fig. 263a in Hesse 1938: 864 and Fig. 3B) very short, only a very little longer than joint 2; joint 3 about twice as long as joints 1 and 2 combined, about $2\frac{2}{3}$ as long as broad, its subterminal spine short, but rather stoutish; palps about as long as antennal joint 3, but not easily seen at base of proboscis; proboscis about 1,08 mm long.

Wings hyaline, iridescent, with a very faint whitish subopacity in certain lights; veins yellowish brown; middle cross vein at a little more than basal third (6: 15) of discoidal cell; part of third vein between cross vein and second submarginal cell shorter than latter cell; knobs of halteres entirely whitish.

Legs with the left hind one shown in Figure 3D.

From a single ♂ specimen originally erroneously described as the ♀ allotype of *namaensis* Hesse.

Length of body: about 1,88 mm
Length of wing: about 2,4 mm

Distribution

Namaqualand: Kamieskroon (Museum staff, September 1930).

Oligodranes elegans Hesse

Oligodranes elegans Hesse, 1938: 865.

The original description of this species was based on two specimens from Aus in South West Africa, in the British Museum (Natural History). These two specimens were taken to be ♀♀, but in view of the fact that the allotype of *namaensis* Hesse was mistaken by me for a ♀ on account of its broadly separated eyes and that a subsequent re-examination of this specimen, and the discovery of the real ♀ of *namaensis*, proved it to be a ♂ belonging to a previously unsuspected section of *Oligodranes* in which the ♂♂ have separated eyes as in a similar section of the genus *Apolysis*, it is more than probable that I confused the sexes and that the two ♀♀ of *elegans* may prove to be two ♂♂. This suspicion is supported by the fact that the ♂♂ of all the known South African species of *Oligodranes* are mainly or predominantly black and that the known ♀♀ have more extensive yellow colouring on the body or are even predominantly yellowish.

On the other hand the fact that the *elegans* specimens, according to my original description, have a more distinct medial frontal depression and also an anterior frontal depression however indicates a ♀ sex.

REVISED DESCRIPTIVE KEY TO ALL THE KNOWN SOUTH AFRICAN SPECIES OF *Oligodranes*

♂♂

1 (*a*) Eyes in actual contact above for a relatively long distance, their upper facets distinctly much coarser than lower ones; frontal triangle or frons anteriorly usually more extensively pallid or yellowish or appearing yellowish in certain lights; legs (cf Fig. 3C) usually relatively longer, more slender, the first posterior tarsal joint usually longer, distinctly more than half length of the tibia 2

(*b*) Eyes broadly separated above, nearly or about 1⅔ to about 2 times width of ocellar tubercle, their upper facets not coarser than lower ones; frons in front not or less extensively pallid and, if yellowish at all, then only narrowly so along upper margin of buccal cavity; legs (cf. Fig. 3D) on the whole shorter, stouter, the first posterior tarsal joint sometimes scarcely, or only a little more than, half length of the tibia 5

2 (*a*) Hairs on body and legs shorter, sparser, less dense, more inconspicuous; knees distinctly much paler, more distinctly yellowish; line of contact between eyes not, or less, deeply impressed; palps shorter, not conspicuous, apparently much shorter than antennal joint 3; hind margins of tergites tending to be relatively more broadly pallid or yellowish 3

(*b*) Hairs on body and legs distinctly longer, denser, much more conspicuous; knees darker, or at least not conspicuously pale; line of contact between eyes distinctly more deeply impressed; palps distinctly more conspicuous, apparently longer, almost, or about, as long as antennal joint 3; hind margins of tergites tending to be more narrowly pallid or yellowish 4

3 (*a*) Hind margins of tergites and sternites, especially former, not or scarcely, or only very narrowly, pallid or yellowish; veins in wings darker, more brownish; distance between middle cross vein and base of second submarginal cell distinctly, or much, longer than latter cell; middle cross vein usually at about, or less than, basal third of discoidal cell; palps slightly longer, subequal to, or only a little shorter than, antennal joint 3 .. .. ♂ *namaensis* Hesse

(*b*) Hind margins of tergites and sternites distinctly more broadly, or more conspicuously, yellowish, sometimes even extensively so; veins in wings paler, more yellowish; distance between middle cross vein and base of second submarginal cell only a little longer, sometimes subequal to, even slightly shorter, than cell itself; middle cross vein usually at a little more than basal third of discoidal cell; palps distinctly much shorter, much shorter than antennal joint 3 .. .. ♂ *triseriatellus* sp. nov.

4 (*a*) Integument of frontal triangle and upper part of genae, sides of face and genae pallid or yellowish; knobs of halteres entirely whitish or pale yellowish; middle cross vein in wings slightly farther away from base of discoidal cell, at about between basal third and fourth; apical stalk of anal cell relatively shorter, much shorter than apical cross vein of discoidal cell; veins in wings paler, more yellowish ♂ *puberulus* sp. nov.

(*b*) Integument of frontal triangle, sides of face, and upper part of genae black, but with greyish white or pale tomentum; knobs of halteres darkened above; middle cross vein in wings slightly nearer base of discoidal cell, at only about basal fourth; apical stalk of anal cell relatively longer, only a little shorter than apical cross vein of discoidal cell; veins in wings darker, more brownish .. ♂ *flavifemoris* sp. nov.

5 (*a*) Humeral angles, upper pleural parts, postalar calli, and narrow hind margins of tergites and sternites distinctly pallid or yellowish; antennal joint 1 shorter, scarcely, or only a little, longer than joint 2; palps shorter than antennal joint 3; proboscis slightly shorter, a little less than 1,5 mm; wing-veins slightly darker ♂ *anomalus* sp. nov. (= ♀ *namaensis* Hesse)

(*b*) Humeral angles, pleurae, postalar calli, and hind margins of tergites entirely black like rest of body, only hind margins of sternites obscurely, very narrowly pallid; antennal joint 1 longer, quite 1½ times length of joint 2; palps longer, quite as long as, or even slightly longer than, antennal joint 3; proboscis slightly longer, quite, or a little more than, 1,5 mm; wing-veins paler, more yellowish *elegans* Hesse (if original specimens be ♂♂)

♀♀

1 (*a*) Body with much or more extensive yellow coloration, the greater part of frons, sides of occiput behind eyes, or even greater part of occiput, broadish sides of thorax in front of wings, postalar calli, even base of thorax, greater part of pleurae, entire scutellum, broad hind margins of tergites and sternites, and greater part of femora more extensively or conspicuously yellow; distance between middle cross vein and base of second submarginal cell in wings subequal to, or longer than, cell itself; hairs on body and legs distinctly shorter and sparser 2

(*b*) Body mainly black or with distinctly less extensive yellow coloration, the greater part of frons, upper half of or entire occiput, greater part of thorax, even on sides, greater part of pleurae, entire or at least basal half of scutellum, and in some forms the legs, black, and only humeral angles, upper part of pleurae just below wings, narrower postalar calli, narrower hind margins of tergites and sternites, and in some forms the femora, being yellow; distance between middle cross vein and base of second submarginal cell usually shorter, or much shorter, than cell itself; hairs on body and legs distinctly longer and denser 3

2 (*a*) Occiput behind ocellar tubercle with a central dark band; base of frons or more often the middle and sides of frons usually dark or black; sides and base of thorax above distinctly less broadly or extensively yellow, the part on each side just above wing-base black and not continuous; yellow hind margins of tergites, though broadened on sides, distinctly much narrower, the black not tending to be broken up to form three longitudinal rows of patches or spots .. .. ♀ *namaensis* Hesse

(*b*) Entire occiput behind ocellar tubercle and eyes and entire frons (excepting sometimes a narrow median spot or line at about middle) yellow; sides and base of thorax above distinctly more broadly and extensively yellow, the part on each side above wing-base continuously yellow, but above it with a rather conspicuous round black spot confluent with black discal part; yellow on abdomen much more extensive, the black basal parts of tergites tending to be reduced and broken up by the yellow to form three longitudinal rows of black spots or patches, becoming smaller posteriorly .. .. ♀ *triseriatellus* sp. nov. (and forms of it)

3 (*a*) Frons anteriorly, lower half of sides of head behind eyes, humeral tubercle, postalar calli, hind part of scutellum, propleural part, middle and hind part of pleurae, and hind margins of tergites and sternites pallid or yellowish; interocular space on vertex at least 2½ times width of ocellar tubercle; veins in wings darker, yellowish brown or brownish; knobs of halteres entirely very pale yellowish white to ivory whitish; hairs on body slightly denser and longer 4

(*b*) Head and body, especially thorax, scutellum, pleurae, and abdomen above, entirely black, only narrowish or obscure hind margins of sternites pallid; interocular space on vertex narrower, only about 2 times width of tubercle; veins in wings more yellowish; knobs of halteres more yellowish or even tinged slightly brownish above; hairs on body sparser and shorter .. *elegans* Hesse (if original specimens be ♀♀)

4 (*a*) Legs entirely dark or blackish brown, only apices of coxae and extreme apices of femora yellowish; head below mainly dark or black, especially hinder half; yellowish hind margins of tergites distinctly narrower, very much narrower than half length of tergites; antennal joint 1 appearing shorter, usually less than twice length of joint 2; wings scarcely or not faintly tinted milky whitish .. ♀ *puberulus* sp. nov.

(*b*) Legs with the greater part of, or entire, coxae and femora yellow, only upper surfaces of front and hind femora basally and apically, or only apically, darkened to a variable extent; head below mainly or entirely yellowish; yellowish hind margins of tergites distinctly broader towards apex, almost or only a little narrower than half length of tergites; antennal joint 1 slightly longer, at least twice length of joint 2; wings distinctly, though faintly, tinted more milky whitish
♀ *flavifemoris* sp. nov. (and forms of it)

SUMMARY

In this paper 14 species of the genus *Phthiria* (subfamily Phthiriinae) are dealt with and of these 9 are described as new. A new variety of an already described species is added. Supplementary redescriptions of some species, previously inadequately described or described from one sex only, are given, and the synonymy of some others, described by me in 1938, is established.

In the two genera *Apolysis* and *Oligodranes*, which Hull transferred to the subfamily Usiinae in 1973, 12 new species of the former and 4 of the latter are described. As in the case of *Apolysis* it has been found that the ♂♂ of some South African species of the genus *Oligodranes* are dichoptic like the ♀♀.

To supplement the descriptions three figures portraying heads, antennae, wings and legs of some species are given.

Revised and descriptive keys to all the known South African species of the three genera dealt with are also given.

ACKNOWLEDGEMENTS

In the preparation of this revision my thanks are due to Dr B. Stuckenberg of the Natal Museum for submitting certain specimens of *Phthiria* from Natal for identification; to the late Mr C. Thorn, a Technical Assistant of the South African Museum, who accompanied me on various collecting trips to Namaqualand and the North-western Cape and who collected many species of Bombyliidae frequenting flowers; and lastly to Mr H. Zinn, the other Technical Assistant, who made many collecting trips with me to the Karoo and adjacent parts and whose contributions to the bombyliid collections in the Museum are second to none.

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INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

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ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.

A. J. Hesse

ADDITIONS TO THE SOUTH AFRICAN SPECIES OF PHTHIRIINAE AND USIINAE (DIPTERA: BOMBYLIIDAE) WITH KEYS TO ALL THE KNOWN SPECIES

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